23.1.20

STUDIES ON MESOZOIC AND CAINOZOIC DINOFLAGELLATE CYSTS

R. J. DAVEY, C. DOWNIE,
W. A. S. SARJEANT & G. L. WILLIAMS

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Supplement 3
LONDON : 1966

STUDIES ON MESOZOIC AND CAINOZOIC DINOFLAGELLATE CYSTS

By
ROGER JACK DAVEY
(Dept. Geology, Nottingham University)
CHARLES DOWNIE, Ph.D.
(Dept. Geology, Sheffield University)
WILLIAM ANTONY SWITHIN SARJEANT, Ph.D.
(Dept. Geology, Nottingham University)
and
GRAHAM LEE WILLIAMS, Ph.D.
(Dept. Geology, Sheffield University)

26 Plates; 64 Text-figures

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Supplement 3
LONDON : 1966

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

In 1965 *a separate Supplementary series of longer papers was instituted, numbered serially for each Department.*

This paper is Supplement No. 3 *of the Geological (Palaeontological) series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

© Trustees of the British Museum (Natural History) 1966

TRUSTEES OF THE
BRITISH MUSEUM (NATURAL HISTORY)

Issued 20 *December,* 1966 *Price £7*

STUDIES ON MESOZOIC AND CAINOZOIC DINOFLAGELLATE CYSTS

By R. J. DAVEY, C. DOWNIE,
W. A. S. SARJEANT & G. L. WILLIAMS

CONTENTS

SYNOPSIS

The morphology of fossil dinoflagellate cysts is discussed ; the cysts are shown to fall into three broad groups (" proximate ", " chorate " and " cavate "), which are interpreted as indicating different modes of formation. New terms are proposed, to enable more precise description of cyst morphology. The principal genera are reconsidered, in the light of new information from studies of assemblages from the Cretaceous (Speeton Clay and Chalk) and Eocene (London Clay) of England. 27 new genera are proposed and emendations are given to the diagnoses of 16 existing genera ; 64 new species are described and the diagnoses of nine existing species are emended. In addition, the generic allocation of other species already

described, from all stratigraphic levels in the Mesozoic and Cainozoic, is reviewed and generic transfers are proposed where necessary. The resultant picture of the stratigraphic distribution of genera and species emphasizes the value of these microfossils as stratigraphic indices.

I. INTRODUCTION

DURING the last few years, research into the nature and distribution of fossil dinoflagellate cysts has been very active, stimulated by realization of the potential value of these microfossils in the correlation of marine strata and by their biological interest. The great bulk of recent researches has been made by French and German palynologists, notably Deflandre, Valensi, Eisenack and Gocht.

In Britain, a brief period of interest followed Ehrenberg's initial discovery of these fossils in flints and his visit to England in 1838: however, after 1850, no further attention was paid to these fossils for a century. In 1957 Downie described a number of types from the Upper Kimmeridge Clay (Kimmeridgian): this was the first study of British Jurassic dinoflagellates. Subsequently Sarjeant, in a series of publications, has described assemblages from the Cornbrash, Oxford Clay, Corallian and Ampthill Clay (Callovian to Oxfordian) : species described by this author (1962) from the Cotham Beds (Rhaetic) include the earliest known clearly tabulate cysts. The distribution of dinoflagellate cysts in the Lias has been studied by Wall (1965).

The first British Lower Cretaceous assemblage to be described was from the Hauterivian section of the Speeton Clay (Neale & Sarjeant 1962), species from other levels of the Speeton Clay are described herein. An assemblage from the Cambridge Greensand (Middle Cretaceous) has been described by Cookson & Hughes (1964). Since 1850, no further work has been published on the Upper Cretaceous : the first results of studies by Davey, at present in progress, are included in the present work.

No British Tertiary assemblages have yet been described. Dinoflagellate cysts from the London Clay (Eocene) have been mentioned by Eagar & Sarjeant (1963) and figured by Mackó (1963), but the first extended study was that made by G. L. Williams (thesis, 1964), of which results are given herein.

No Quaternary assemblages have been described ; work by Deflandre referred to by West (1961) has not been published.

There has been considerable progress in recent years in our understanding of the nature of these cysts, largely as a result of the studies of Evitt (1961, 1963, Evitt & Davidson 1964). He has elucidated some of their fundamental structures and drawn attention to the importance of the cyst openings (archaeopyles) and of structures representing a reflected tabulation, thus effectively demonstrating the affinity of many formerly problematic genera (the " hystrichospheres " *sensu stricto*).

This paper comprises a full-scale review of certain of the principal genera of fossil dinoflagellate cysts, involving extensive revision of generic diagnoses and the erection of new taxa. In addition, new genera and species are described from various Mesozoic and Tertiary horizons.

II. THE MORPHOLOGY, TERMINOLOGY AND CLASSIFICATION OF FOSSIL DINOFLAGELLATE CYSTS

By C. DOWNIE & W. A. S. SARJEANT

In the description of fossil dinoflagellates in the past, the terms used have been largely borrowed from modern plankton descriptions. This is appropriate enough : however, as studies of fossil dinoflagellates have developed, structures have been discovered for which no terms exist and the use of descriptive terms, without specification of precise meanings, has produced, on the one hand, ambiguity, on the other hand, the failure to distinguish between different, albeit broadly similar, structures—cf., for example, past usage of the terms "spine" and "tube" in description of appendages.

The work of Evitt (1961, 1965, in press) has gone some way towards the establishment of precise terms for some morphological characters. In the present work, a number of new terms are proposed which, it is hoped, will form a workable basis for future descriptions.

In addition, the existence of broad groupings of morphologically similar dinoflagellate cysts has become apparent : these groupings appear to have considerable stratigraphic meaning. The classification at present in use is criticized for not taking cyst structure into account.

MORPHOLOGY AND TERMINOLOGY. (1) Cysts and Motile Stage Thecae.

Evitt & Davidson (1964) have described the process of cyst formation in some Recent dinoflagellates and have shown that these resting cysts are of types closely resembling some of the most common fossil species. They conclude that most, if not all, of the fossil remains of dinoflagellates are cysts. These cysts are smaller than the motile stage cell and are formed by the deposition of an ellipsoidal or spherical wall some distance inside the motile stage envelope (or theca if hardened). This wall in fossil and Recent cysts is often seen to be constructed of two layers, which we propose to call the endophragm and the periphragm. The outer layer, or periphragm, usually carries extensions, either in the form of spines or as lists, which extend out to the position of the formal thecal wall and appear to have acted as supports during the period of cyst formation (Text-fig. 1).

Many kinds of fossil dinoflagellate cysts are equipped with a special opening which functions when the cyst contents are to be released. These openings, called archaeopyles by Evitt, generally have a definite polygonal shape and are fixed in location in any particular species. Their presence in a fossil demonstrates that it is a cyst. Fossil remains of potentially motile dinoflagellates lack an archaeopyle and have a cingulum, or transverse furrow, in the form of a continuous spiral groove which has no impediments such as spines and septae crossing its track, indicating that this was the former position of the transverse flagellum (Text-fig. 2).

Tabulation, which is a striking feature of the living armoured dinoflagellates, can also be represented in cysts, often highly modified, but its presence or absence is not determinative in distinguishing cysts from motile stage thecae.

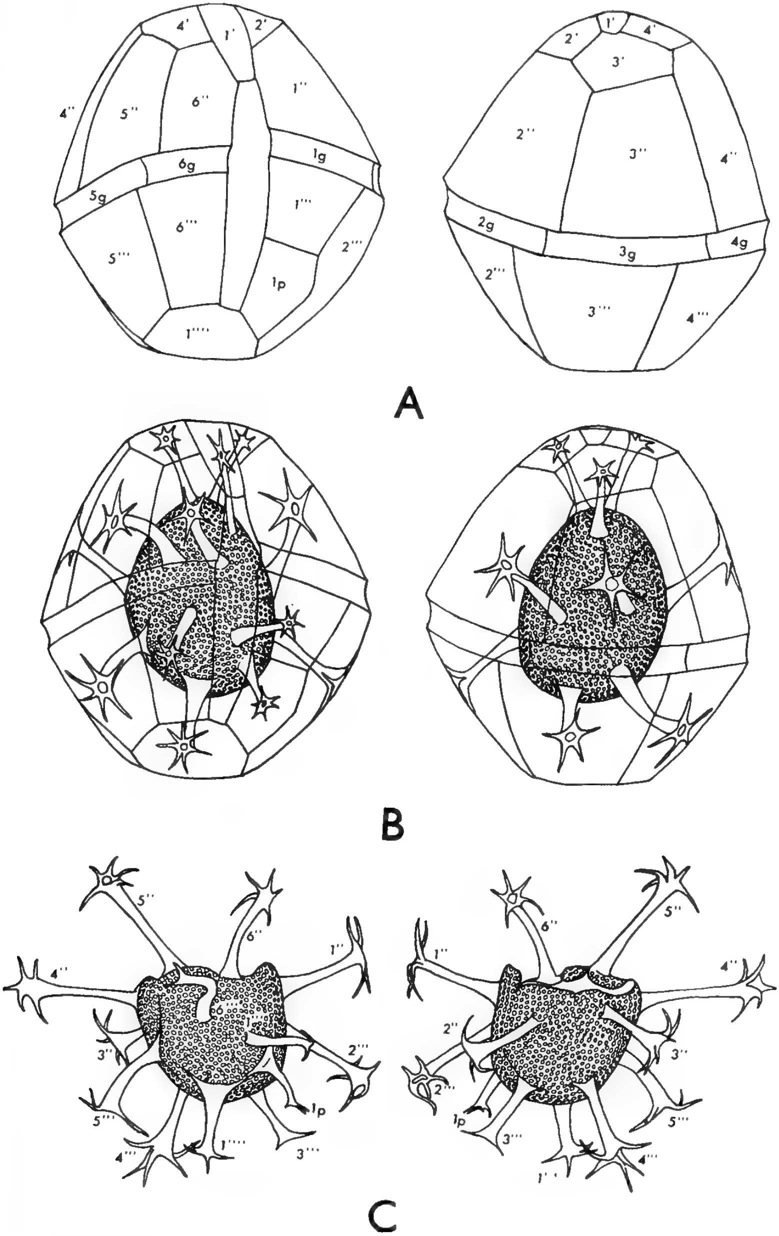


FIG. 1. *Oligosphaeridium vasiformum* (Neale & Sarjeant), a typical chorate cyst, showing the presumed method of cyst formation. A, The probable original tabulation of the dinoflagellate, which corresponds to that of *Gonyaulacysta*. (The apical tabulation is wholly speculative.) B, The cyst forming within the dinoflagellate theca, attached to the cell membrane by its processes. C, The abandoned cyst as found, with an apical archaeopyle. [After Sarjeant (1965) reproduced by permission of the Editor of " Endeavour ".]

The term " ambitus " applied to dinoflagellates refers to the test outline viewed from the dorsal or ventral side.

(2) The Morphology of Motile Stage Thecae.

Modern dinoflagellates may be thin-walled or may have robust cellulosic tests (thecae), which are clearly divided into fields by sutures in the tabulate genera. Text-fig. 2A shows a test of this type and indicates the terminology used to describe it. Other morphological structures are shown in Text-figs. 3, 4.

(3) Fossilized Motile Thecae.

Very few fossil dinoflagellates could be considered as the remains of motile stage thecae. The strongest claims can be made for some species of *Peridinium* and *Gymnodinium* from the Upper Cretaceous which lack archaeopyles and show no other structures characteristic of cysts.

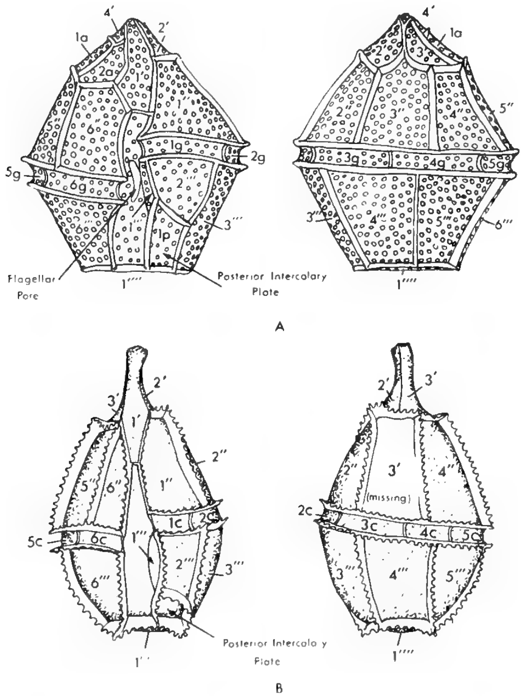


FIG. 2. The tabulation of a modern dinoflagellate, compared with that of a proximate dinoflagellate cyst. A, *Gonyaulax polyedra*, a dinoflagellate of present day warm and temperate seas. After Kofoid. B, *Gonyaulacysta jurassica*, from the Upper Jurassic ; a proximate cyst with a precingular archaeopyle. [After Sarjeant (1965) reproduced by permission of the Editor of " Endeavour ".]

(4) The Morphology of Cysts.

(a) *Major Cyst Types.*

The cysts are always smaller than the motile cell and can be grouped according to their degree of contraction. The degree of contraction also affects their general appearance, for those which are most condensed bear little superficial resemblance to the parent cell, whereas those that are near the motile cyst in size closely resemble it in appearance. Consequently two groups of cysts are here recognized, the *chorate* (or condensed) cysts and the *proximate* cysts.

In both these groups of cysts, the two wall layers are generally in close contact and only rarely come apart, but there is a third group, here called the *cavate* cysts, in which a space, or spaces of notable size, occurs between the periphragm and endophragm. This space is here named the pericoel ; it separates an inner body (capsule) formed by the endophragm from the outer cyst wall, the cavity of this inner body is called the endocoel.

(b) *Cyst Openings.*

The polygonal openings found on cysts have been called pylomes by Eisenack. This is, however, a broad term and includes also circular or slit-like openings which are in no way characteristic of, or confined to, the dinoflagellates. Evitt's term archaeopyle refers specifically to those kinds of pylome which characterize some dinoflagellate cysts. They are usually polygonal and precisely located and orientated on the test, corresponding to specific locations in the structure of the *tabulate* dinoflagellates. The terminology used here generally corresponds to that proposed by Evitt (1961, text-figs. 5–8), with the addition of *epitractal*, for archaeopyles formed by breakage parallel, and immediately anterior to, the cingulum (equivalent to *epithecal* archaeopyles of Norris 1965), and *cingular*, for archaeopyles formed by

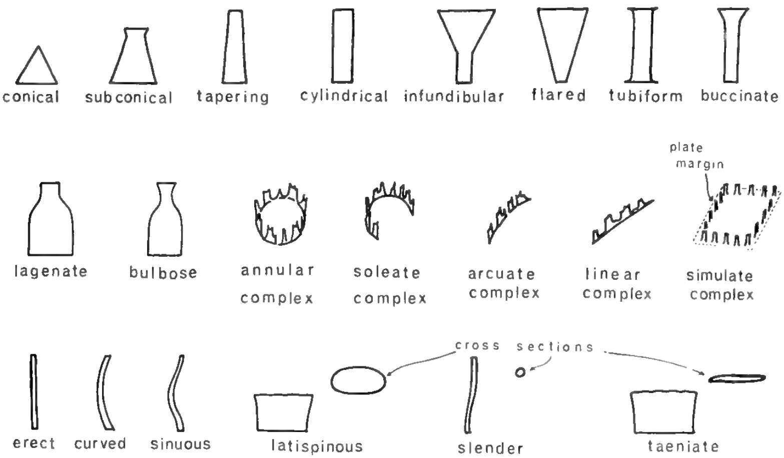


FIG. 3. Illustrations of the terms used to describe the overall shape of the processes and process complexes. The distal end is uppermost in each case.

breakage along and within the cingulum. Apical archaeopyles are called *haplotabular* when they consist of a single plate and *tetratabular* when they have four.

(5) Proximate Cysts.

The proximate cysts are an important group, which have always been recognized as dinoflagellates because their resemblance to modern forms is very close. Nevertheless, although all the features of tabulation may easily be determined on good specimens, they are not motile thecae, but cysts. The terms epitheca and hypotheca used for motile stages, are therefore inappropriate. It is here proposed that their cyst equivalents should be termed *epitract* and *hypotract*, names suggested by G. L. Williams (thesis, 1964).

Contraction in the formation of the proximate cyst is generally to about $\frac{1}{2}$ or $\frac{2}{3}$ of the original volume; this can roughly be gauged by the height of the periphragm spines or lists. The ratio $\frac{\text{Radius of endocoel}}{\text{Radius overall}} = 0{\cdot}8$ constitutes a rough limit to the proximate cysts.

The periphragm often forms extensions which bear a close relationship to the presumed tabulation of the motile stage theca. These extensions are nearly always sutural (i.e. reflecting the site of the sutures on the motile stage) and most often consist of continuous crests or lists, often with serrate or denticulate edges. Less commonly, lines of small solid spines or tubercles mark the reflected sutures.

Subdivision of the proximate group of cysts is based on a number of features among which the reflected tabulation, the overall shape of the test (i.e. elongation, number of horns) and the nature of the archaeopyle are important.

Typical of the proximate cysts is the genus *Gonyaulacysta*. The group as a whole is more characteristic of Upper Jurassic–Lower Cretaceous than of later strata.

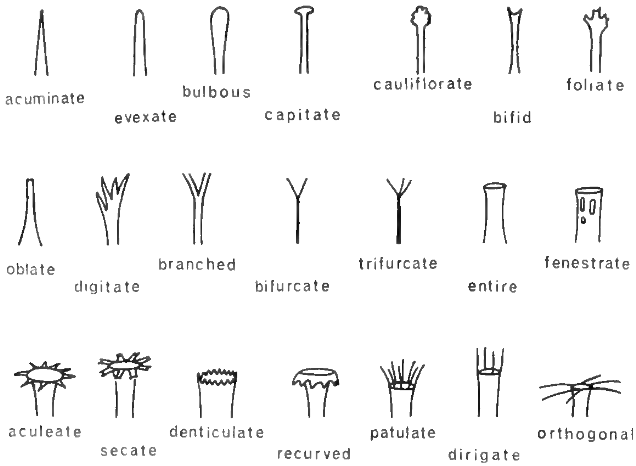


FIG. 4. Illustrations of the terms used to describe the various kinds of distal termination of the processes.

(6) Chorate Cysts.

Chorate cysts in general resemble *Hystrichosphaeridium* and include all the typical hystrichospheres. They are distinguished from proximate cysts by the greater contraction that took place during cyst formation, for the cyst has only about $\frac{1}{3}$ the volume of the motile cell and the contraction ratio $\frac{\text{Radius of endocoel}}{\text{Radius overall}}$ is typically about 0·6. As a consequence of this greater contraction the tabulation is often only indirectly determinable, if at all, and the general appearance is not dinoflagellate-like. Furthermore, the outgrowths of the periphragm are longer and often exceed in length the endocoel radius. These outgrowths are commonly spine-like, and are either located from the site of the sutures (sutural appendages) or within the edges of the plates (intratabular appendages).

Intratabular appendages occur in various ways, but are usually either hollow or grouped in patterns related to the tabulation. The hollow processes are open at the distal end in *Hystrichosphaeridium*, but in *Cleistophaeridium* they are closed distally. So far, no species definitely identified as a dinoflagellate cyst has spines which open into the endocoel.

The open-ended processes have various kinds of distal openings, which may flare like trumpets or constrict ; various kinds are illustrated in Text-figs. 3, 4. In some cyst groups the processes may be connected distally by narrow solid rods (*trabeculae*) : in others a thin membrane (*ectophragm*) may still persist between the distal ends. The ectophragm must have been laid down very close to the motile cell envelope. Often only one appendage occurs on each plate, but there may be more, and when the appendages are very numerous the tabulation may not be determinable at all.

Other kinds of intratabular appendages are often found to be solid and to occur in groups (see Text-figs. 3, 4). *Polystephanephorus* is characterized by annulate groups, and *Areoligera* by coronate and soleate groups. Usually no more than one group is found associated with one plate so that they are useful in determining the tabulation.

Sutural elements may consist of rows of spines or of spines situated only at plate corners (gonal spines), but commonly these spines have merging bases forming continuous flanges or lists as in the proximate cysts. These elements are usually solid but small pyramidal cavities may develop at the base of the gonal spines, which in *Hystrichosphaeropsis* begin to run together to form a larger, more continuous cavity.

Several sub-divisions of the chorate group of cysts are found to be useful. The *typical chorate* cysts are represented by highly condensed forms like *Hystrichosphaeridium* and *Cleistosphaeridium* with cylindrical or spine-like processes. Their condensation ratio is about 0·5 or 0·6 and the outgrowths are intratabular. *Proximochorate* cysts include forms like *Hystrichosphaera* which have generally lower condensation ratios (0·6–0·8) and sutural outgrowths which more readily indicate the tabulation. *Raphidodinium* is a highly condensed representative. The *trabeculate*

chorate cysts are represented by *Cannosphaeropsis*; and *Membranilarnacia* is typical of the *membranate* group.

A *pterate* group can also be recognized with *Wanea* as a representative, its main characteristic being its pronounced equatorial outgrowth in the form of solid processes linked distally or in mesh-like fashion. The *marginate* cysts form a group, typified by *Areoligera*, consisting of chorate cysts whose outgrowths are characteristically localized on the lateral margins, leaving the dorsal and more often the ventral surfaces free of large outgrowths.

Chorate cysts have a very long history, but they are more important in the Upper Cretaceous and Tertiary than at any other time.

(7) Cavate Cysts.

In some forms already mentioned, small pericoels have been found between the endophragm and periphragm. In the cavate group of cysts, the pericoel is a dominant feature, so that the body consists of an inner body (capsule) formed by the endophragm and an enclosing body, formed by the periphragm, often of quite a different shape.

The inner body is usually ellipsoidal, thick walled, with a smooth or granular surface. It may have an archaeopyle but rarely shows any sign of tabulation. In a few forms spinous projections bridge the gap between the endophragm and the periphragm, but in many the cavity is more or less continuous and contact between the two is either not apparent or occurs only at the mid-ventral line. The periphragm is usually thinner and often smooth. It does however quite often have an archaeopyle and may show a tabulation marked by sutural lines, or by intratabular spine pallisades as in *Wetzeliella*. The overall shape is an important feature in these cysts, especially the number and positions of the horns on the periphragm.

A number of sub-groups are recognized depending on the degree of continuity of the pericoel. In typical cavate cysts like *Deflandrea phosphoritica* there is only one large pericoel extending over nearly all the body. In bicavate cysts there is a wide zone of contact round the equator which divides the pericoel into an apical and antapical part; *Triblastula* is typical of this group. *Stephodinium* represents a small group (the *pterocavate* cysts) with a pronounced equatorial pericoel. Small pericoels may occur in other groups such as the apical pericoels in some proximate cysts, the gonal pericoels in some *Hystrichosphaera* species.

(8) Other Cyst Groups.

In addition to the three main groups discussed so far one must recognize the existence of groups of fossil dinoflagellates with calcareous tests and with siliceous tests. Neither of these groups is being considered in this paper, although most appear to be non-motile and probably encysted.

Classification. Eisenack (1964) published a classification of fossil dinoflagellates which is by far the most comprehensive classification yet attempted. In this paper he adopts a botanical system, which is welcomed. However, his classification

cannot be considered satisfactory, because he does not allow enough importance to the fact that we are dealing with cysts.

Evitt & Davidson (1964), Deflandre (1962) and Norris (1965) have cogently stated the taxonomic problem that arises because so little is known about the encystment of living species of dinoflagellates. Currently the classification of living species and genera is based on the tabulation and appearance of the motile stage cell, but it is now known (Evitt & Davidson 1964) that similar motile stages can produce grossly different cysts and an extensive reclassification is likely to ensue when more work has been done on encystment. It is therefore unsatisfactory to press fossil cysts into a taxonomic system based largely on living motile stages as Eisenack has done, when we know so little about the life cycles and important reclassification of the living forms is impending.

The frequent dissimilarity between the motile and cyst stages means that attribution of a cyst to a species based on a motile stage can only be confidently asserted on the direct evidence of cultures or on the circumstantial evidence of close geographic association of certain cyst types with certain motile stage types. Neither of these possibilities is available to the palynologist who at the most can hope to identify a fossil cyst with a Recent one by morphological comparison. In an overwhelming number of instances he can expect to find no exact counterpart, and his classification must be a classification of cysts.

It is hoped to deal more thoroughly with the classification of fossil dinoflagellate cysts in a separate publication where the whole range of cyst types can be considered adequately.

III. STRATIGRAPHY AND HISTORICAL BACKGROUND

a. The Speeton Clay

By W. A. S. SARJEANT

The Speeton Clay is the lowest of the three horizons principally dealt with in this work. Two boreholes were put down through the Speeton Clay during the summer of 1960 by Koninklijke Shell Exploratie en Produktie Laboratorium, Rijswijk, The Netherlands. The first of these, Shell Speeton No. 1, was sited near Speeton Beck (grid ref. TA.151753) and reached a depth of 135·25 metres (443 ft. 11 in.); the second, Shell West Heslerton No. 1, was put down at West Heslerton, some 1·4 miles west of Speeton, reaching a depth of 117 metres (383 ft. 4 in.) without bottoming the Lower Cretaceous. Through the courtesy of Shell Internationale Research Maatschappij N.V., The Hague, Netherlands, specimens were made available for micropalaeontological and palynological study to various specialists. Results of study of the Speeton Clay ostracod faunas have been published by Neale (1960*a*, 1962*a*), Neale & Kilenyi (1961) and Kaye (1963*a*, 1963*b*, 1964*a*). These authors also published accounts of the outcrop stratigraphy (Neale 1960*b*, 1962*b*; Kaye 1964*b*); their accounts of the stratigraphy and ostracod faunas of the boreholes are currently in press.

The assemblages of fossil microplankton proved unexpectedly rich. They are dominated by dinoflagellate cysts, acritarchs being relatively infrequent. Studies have to date been concentrated on the assemblages from the West Heslerton borehole, a brief account of some new species from a Hauterivian horizon having already been published (Neale & Sarjeant 1962). The holotypes of the species described in that paper, formerly in the collections of the Sedimentology Research Laboratory, University of Reading, are now lodged in the British Museum (Natural History) under the following numbers:

Species	Reading Nos.	B.M.(N.H.)
Heslertonia heslertonensis (formerly *Gonyaulax*)	44Y/8/10	V.51713(1)
Gonyaulacysta cretacea (formerly *Gonyaulax*)	44Y/4/21	V.51711(2)
Cribroperidinium sepimentum	44Y/7/7	V.51712 (1)
Gardodinium albertii	44Y/1/28	V.51709(2)
Pseudoceratium (*Eopseudoceratium*) *gochti*	44Y/1/36	V.51709 (4)
Muderongia crucis	44Y/4/1	V.51711(1)
Heliodinium patriciae	44Y/3/3	V.51710(1)
Oligosphaeridium vasiformum (formerly *Hystrichosphaeridium*)		
Holotype	44Y/1/34	V.51709(3)
Paratype	44Y/1/26	V.51709(1)
Oligosphaeridium macrotubulum (formerly *Hystrichosphaeridium*)	44Y/7/20	V.51712(2)
Systematophora complicata	44Y/4/22	V.51711(3)

Subsequently, examination of asssemblages has been extended upwards into the Barremian. In the chapters which follow, the results are given of studies by R. J. Davey and the writer on the dinoflagellate cysts from five assemblages in the West Heslerton No. 1 Borehole, as follows :

Depth	Character of Sediment	Stage
19·25/50 metres	Soft, medium dark grey (N4) to live grey (SY4/1) clay, containing much pyrite.	Upper Barremian (Middle part)
39·00/25 metres	Softish, medium (N5) to olive grey (5Y5/1) clay, pyritic, with some shell fragments.	Middle Barremian (Cement Beds)
42·50/75 metres	Lithology as last.	Lower Barremian (top)
99·25/50 metres	Hard, medium olive grey (5Y5/1) siltstone, laminated and pyritic.	Middle Hauterivian
103·25/50 metres	Well-laminated olive grey (5Y6/1) pyritic clay, rather streaky, with shell fragments.	Middle Hauterivian

(The numbers in parentheses are the American Rock Colour Chart numbers.) For further stratigraphical information, see forthcoming paper by Neale & Kaye.

b. The Lower Chalk

By R. J. DAVEY

Fossil microplankton from the Upper Chalk (Senonian) of Great Britain were first described in the mid-nineteenth century by a group of amateur microscopists, namely Mantell, Reade, Deane, White, Bowerbank and Wilkinson. After these initial studies no subsequent work was performed in Great Britain on Upper Cretaceous microplankton until 1964, when Cookson & Hughes published a paper on microplankton from the Cambridge Greensand, of presumed basal Cenomanian age. The work referred to in the following chapters, on microplankton assemblages from the English Lower Chalk (Cenomanian), is part of a larger study of the Cenomanian assemblages throughout the world.

Specimens quoted in this paper as being of Cenomanian age have all been obtained from samples from H.M. Geological Survey Borehole at Fetcham Mill, Leatherhead, Surrey (National Grid Reference, TQ.158565). At this locality the Cenomanian is 197 feet thick and lies conformably on the Upper Greensand. The basal Cenomanian is a grey, glauconitic impure chalk containing a relatively high percentage of clay minerals. The percentage of clay minerals progressively decreases towards the top of the stage where the Cenomanian is a hard, almost pure, white chalk. A full account of the stratigraphy appears in the Geological Survey Bulletin No. 23.

Ten samples, at twenty foot intervals, were analysed for their organic-shelled microplankton content. The microplankton content was quite rich and fairly well preserved. Cysts of dinoflagellates were predominant over acritarch remains, and spores and pollen were relatively rare.

c. The London Clay

By G. L. WILLIAMS & C. DOWNIE

Dinoflagellate cysts (hystrichospheres) were first briefly recorded from the London Clay by E. W. Wetherell (1892). No further work was done on them for over 60 years. They first came to the attention of one of us (C.D.) in 1958, when Murray Hughes of the Geological Survey sent for identification a number of species picked out from washed foraminifera preparations which had come from London Clay at Isleworth, Middlesex. Mr. D. Curry (1958 : 56) had however previously exhibited hystrichospheres from the Eocene at a meeting of the Geologists' Association in November 1957. Subsequently Eager & Sarjeant (1963) recorded *Hystrichosphaeridium* similarly obtained from Berkshire. Mackó (1963) figured a variety of forms from the London Clay without identifying any of them conclusively.

The first systematic work on the dinoflagellates of the formation was begun in 1960 in Sheffield by G. L. Williams. His thesis (1963) dealt with all the planktonic dinoflagellates and acritarchs in the samples examined. Many of these were derived from older formations and are being described elsewhere ; the indigenous acritarchs and dinoflagellates will be listed here, but the acritarchs will not be described. Dinoflagellates belonging to *Hystrichosphaera*, *Haplosphaeridium*, *Cleistosphaeridium*, *Hystrichosphaeridium* and allied genera are treated by Davey & Williams in Sections IV and V of the present work.

Stratigraphy. The London Clay is confined to two areas in Southern England, the London and Hampshire Basins respectively. They formed one continuous basin of deposition during Eocene times but subsequent orogenic movements and erosion have given rise to the intervening Wealden Dome separating the two main outcrops of the London Clay. The term basin when speaking of the two areas is therefore used in a structural sense referring to the present day conditions only. There is close similarity between the lithology of the London Clay of the western margin of the London Basin and of the Hampshire Basin where the " typical " stiff blue grey clay is increasingly replaced by arenaceous beds, loamy and sandy bands being common.

To the east of the London Basin, the blue clay reaches its greatest thickness, at Sheppey, where it is estimated to be over 500 feet thick with little change in lithology throughout. Collecting was undertaken at three places, Studland Bay in Dorset, Whitecliff Bay in the Isle of Wight, both in the Hampshire Basin, and Sheppey in the London Basin. In addition, Professor H. L. Hawkins kindly provided samples from borehole cores from the Enborne Valley, lying in the west of the London Basin where the lithology shows striking similarities to that of the Hampshire Basin.

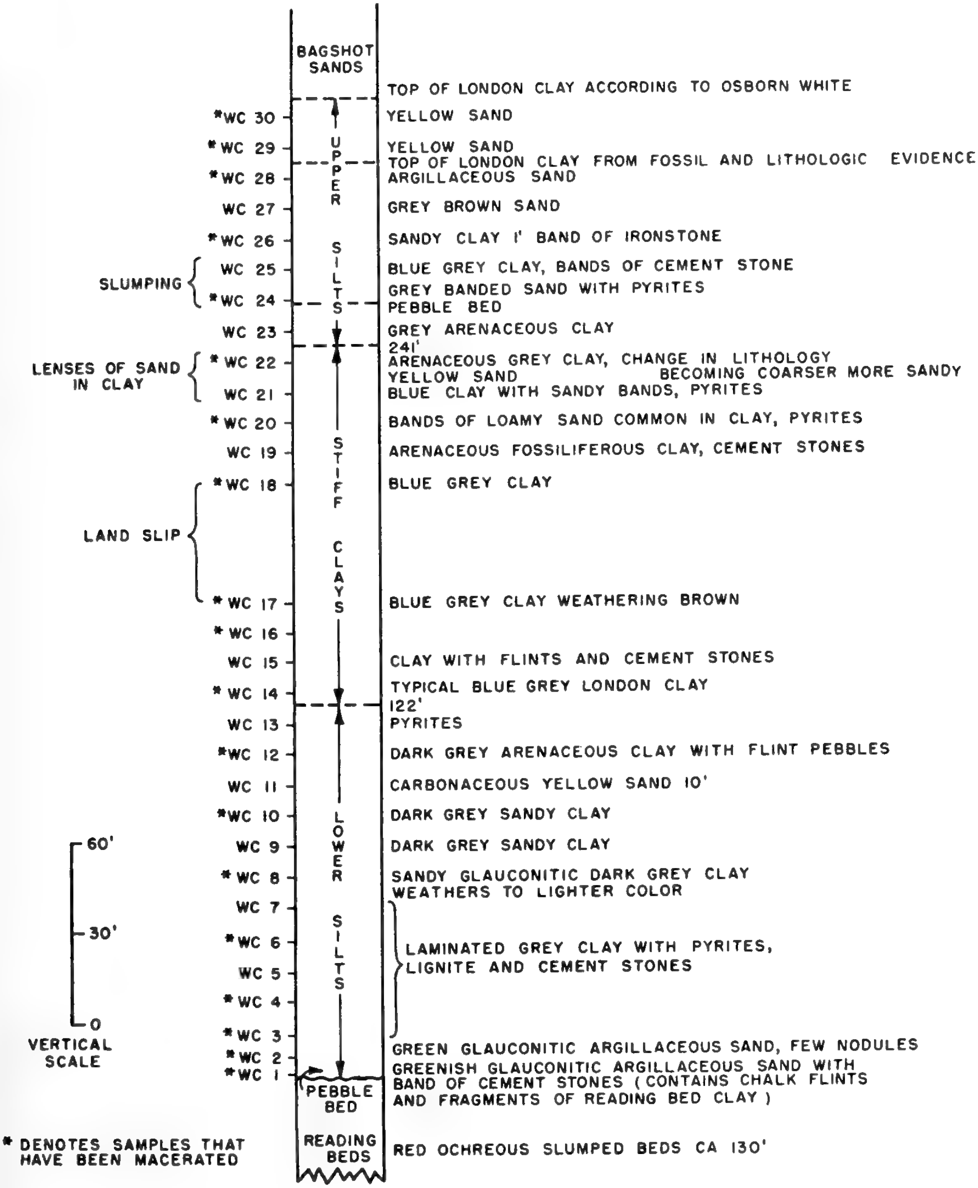


FIG. 5. Succession of the London Clay at Whitecliff Bay, showing the location of samples.

STUDLAND BAY. One of the most westerly outcrops of the London Clay is found at Studland Bay in Dorset, where conditions in the Lower Eocene fluctuated between marine and fresh-water, being very close to, and at times marking, the shoreline of the London Clay sea. As with all cliff sections of the London Clay, difficulty is experienced in collecting because of slumping. This obscures most of the London Clay but fortunately both lower and upper junctions with the Reading and Bagshot Beds are exposed.

Because of the poor exposures, samples could only be taken haphazardly, three (ST. 1–3) being collected within 10 feet of the base, and one (ST. 4) from only three feet below the junction with the Bagshot Beds. The London Clay at Studland is, at the base, an arenaceous yellow brown clay passing upwards into a friable yellow argillaceous sand ; the succeeding Bagshot Beds are almost pure quartz sands, bright yellow in colour and partly consolidated.

ISLE OF WIGHT. The exposures of London Clay in the Isle of Wight at Alum Bay and Whitecliff Bay are of importance because they give the only continuous exposures through the whole London Clay, from the junction with the Reading Beds to the base of the Bagshot Sands. The dip of the beds is almost vertical and they strike at right angles to the exposure, thus providing comparatively easy conditions for collecting. The main difficulty is slumping or slipping, which is a common occurrence in the Alum Bay section, less frequent at Whitecliff. Only the Whitecliff section has been studied because it is less affected by slumping and the junction of the London Clay and Bagshot Beds can be more precisely placed.

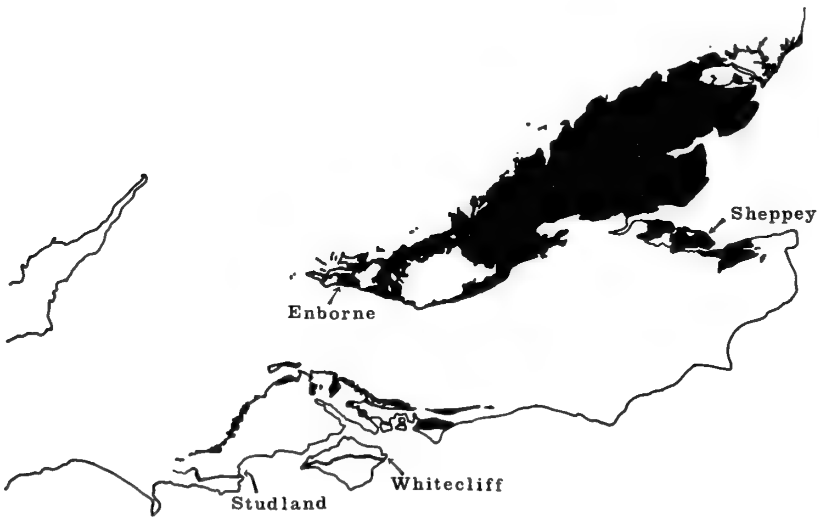


FIG. 6. Map of South-east England, showing in black the outcrop of the London Clay. The localities from which samples were collected are shown by the arrows.

According to the earliest authority on the Eocene of Whitecliff, Prestwich (1847), the thickness of his beds 3 and 4, (which he called the Bognor Beds), is 307 feet. These are equivalent to the London Clay. Bristow (1862) lists a succession but attempts no estimation of thickness. In the revised Isle of Wight Memoir of 1889, the section is not given in detail, but an approximate value of 320 feet for the thickness of the London Clay is quoted by Reid. The pebble bed according to Reid is 255 feet above the base. The first detailed section is attributable to White (1921) who measured a total of 322 feet, with the pebble bed at 285 feet above the base. Since 1921 all authorities including Curry (1958*a*) have quoted this thickness of 322 feet for the London Clay of Whitecliff. In measurements carried out by the authors with a tape measure a value of 300 feet was arrived at for the thickness of the London Clay with the pebble bed at 255 feet. Samples were taken for 315 feet above the base but the two topmost (305, 315 feet) were yellow sands barren of microplankton.

Lithologically, the London Clay at Whitecliff is roughly divisible into three units equivalent to the Lower Silts, the Stiff Clays and the Upper Silts of the Enborne Valley (Hawkins 1954). Within each of these three units alternations of clays and sands with all degrees of intermingling often occur and septarian nodules, lignite and iron pyrites are common throughout. Sample numbers are shown in Text-fig. 5.

ENBORNE VALLEY (Berkshire). In the years 1947–49 a series of borings were sunk in the eastern part of the Enborne Valley, penetrating beds primarily of Eocene age, much of which was London Clay. Professor H. L. Hawkins has kindly allowed us to take samples from cores in his possession. Two boreholes, numbers 11 and 39 whose geographical positions can be seen in Text-fig. 6, were examined.

According to Hawkins (1954), the London Clay of the Enborne Valley is lithologically divisible into three sections, the Lower Silts, the Stiff Clays and the Upper Silts.

From boring number 11, six samples have been examined in detail, one from the Upper Silts, four from the Stiff Clays and one from the Lower Silts. From boring number 39, four samples have been studied, three from the Stiff Clays, one from the Lower Silts. All the samples studied yielded microplankton usually in a good state of preservation (see Text-fig. 7).

SHEPPEY. The London Clay attains its maximum thickness at Sheppey where Davis (1936) has estimated it to be 518 feet. Of this the upper 160 feet are exposed in the Sheppey cliff section running for six miles in an east-south-east direction from Scrapgate in the west to Warden Point in the east. The lithology is a uniform stiff blue grey clay with frequent courses of septaria. The junction with the Bagshot Beds is well exposed in the west where 10 feet of *in situ* Bagshot sand overlies the London Clay ; elsewhere difficulty is caused by large scale slipping and the number of samples collected is less than might have been desired.

Wrigley (1924) proposed five divisions for the London Clay of the London Basin, each characterized by a faunal suite but not zones in the strictest sense. The fifth (uppermost) division is typically sandy with more frequent fossils than blue clay.

TABLE I

	STUDLAND	WHITECLIFF																	ENBORNE 11						ENBORNE 39				SHEPPEY				
	4	1	2	3	4	6	8	10	12	14	16	17	18	20	22	24	26	28	31	41	51	61	71	88	25	35	45	52	1	2	3	4	5
Hystrichosphaeridium tubiferum (Ehr.)	×	×	×	×	×	×	×	×	×	×	×	×	×	×			×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
tubiferum v. *brevispina* nov.										×		×															×	×		×			
salpingophorum Defl.	×		×	×	×	×	×	×		×	×	×	×				×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
latirictum sp. nov.				×		×						×						×	×		×			×									
sheppeyense sp. nov.	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×		×	×	×	×	×		×	×		×	×	×		
Polysphaeridium pastielsi sp. nov.																													×	×	×	×	×
subtile sp. nov.																														×			×
Oligosphaeridium complex (White)	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
pulcherrimum (Defl. & Cooks.)	×	×	×								×				×					×	×			×		×	×			×			
Perisseiasphaeridium pannosum sp. nov.	×			×	×		×			×		×	×	×		×		×		×	×	×	×	×	×	×	×	×	×	×	×	×	×
Litosphaeridium inversibuccinum sp. nov.		×	×	×	×		×	×			×	×				×			×						×		×			×	×		
Cordosphaeridium gracilis (Eis.)	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
inodes (Klumpp)		×								×	×	×																×		×		×	×
multispinosum sp. nov.		×									×																				×		×
fibrospinosum sp. nov.					×																	×			×	×			×	×	×		
exilimurum sp. nov.	×	×		×	×		×		×	×	×	×	×	×		×	×	×						×				×		×	×	×	×
cracenospinosum sp. nov.				×	×																				×	×							
divergens (Eis.)							×			×	×	×		×			×		×	×	×	×	×	×				×	×				
latispinosum sp. nov.																			×								×			×			×
Tanyosphaeridium regulare sp. nov.														×		×										×	×						
Cleistosphaeridium disjunctum sp. nov.	×	×	×	×	×						×	×				×			×	×		×	×	×	×								
diversispinum sp. nov.			×	×	×	×			×	×	×	×	×			×	×	×		×	×	×	×	×	×			×			×		
Diphyes colligerum (Defl. & Cooks.)	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
Homotryblium tenuispinosum sp. nov.																				×	×									×			
pallidum sp. nov.										×		×	×	×							×	×								×	×		×
Adnatosphaeridium patulum sp. nov.				×	×	×	×	×	×	×	×	×		×	×		×	×		×	×	×	×	×			×	×			×		
vittatum sp. nov.																														×	×	×	
multispinosum sp. nov.											×																						
Hystrichokolpoma eisenacki sp. nov.	×	×		×	×		×		×		×	×		×			×	×		×		×		×	×	×		×	×	×	×	×	
eisenacki v. *turgidum* nov.																						×								×			
unispinum sp. nov.						×															×	×											
rigaudae Defl. & Cooks.				×		×	×		×										×							×			×		×		
Membranilarnacia reticulata sp. nov.											×	×	×	×	×	×	×	×			×	×	×	×					×	×	×	×	×
Hystrichosphaera ramosa v. *ramosa* (Ehr.)	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
v. *granosa* nov.				×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
v. *granomembranacea* nov.					×																									×		×	
v. *gracilis* nov.	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
v. *multibreve* nov.			×	×															×		×		×	×								×	
v. *membrancea* nov.		×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
buccina sp. nov.		×	×	×	×				×	×	×	×	×	×			×		×	×	×	×	×		×	×	×	×	×	×	×	×	×
perforata sp. nov.							×					×						×		×			×			×		×			×	×	
cornuta Gerlach						×					×	×	×				×	×	×					×						×	×	×	
laevimura sp. nov.				×							×													×						×			
cf. *cornuta* Gerlach					×							×																			×		
monilis sp. nov.										×		×																		×			

	Studland	Whitecliff																	Enborne 11						Enborne 39				Sheppey				
Achomosphaera alcicornu (Eis.)			×	×		×				×		×	×						×				×	×					×	×		×	
ramulifera (Defl.)			×	×	×	×	×	×	×	×	×	×	×	×	×	×		×	×		×	×	×	×	×					×			
ramulifera v. *perforata* nov.				×	×														×														
Cannosphaeropsis reticulensis Pastiels		×	×			×				×	×			×				×					×	×	×					×			
Nematosphaeropsis balcombiana Defl. & Cooks.						×													×														
Cyclonephaleum pastielsi Defl. & Cooks.										×							×							×									
exuberans Defl. & Cooks.											×									×	×	×											
ordinatum sp. nov.		×		×	×		×							×				×	×		×	×											
divaricum sp. nov.	×	×	×	×	×		×												×			×		×	×	×			×	×		×	
Areoligera coronata (O. Wetz.)												×	×																	×			×
cf. *coronata* (O. Wetz.)																																	×
cf. *medusettiformis* (O. Wetz.)																																	×
cf. *senonensis* Lej. Carp.																																×	
Wetzeliella articulata Eis.				×			×					×					×		×			×	×	×		×			×	×	×	×	×
v. *conopia* nov.																														×		×	
coleothrypra sp. nov.																														×	×	×	×
reticulata sp. nov.																														×			
tenuivirgula sp. nov.																									×					×	×	×	
tenuivirgula v. *crassoramosa* nov.					×																									×			
homomorpha Defl. & Cooks.		×		×		×	×	×	×			×	×	×		×	×	×		×			×	×	×								
homomorpha v. quinquelata nov.				×		×	×		×	×	×	×			×	×			×	×			×	×		×	×						
ovalis Eis.							×																				×	×					
condylos sp. nov.																														×			
similis Eis.		×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×									
symmetrica Weiler	×			×							×								×	×					×	×			×				
symmetrica v. *lobisca* nov.	×			×								×												×					×				
varielongituda sp. nov.							×																						×	×			×
glabra Cooks.																														×	×		×
Deflandrea phosphoritica Eis.	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
phosphoritica v. *australis* Cooks. Eis.																										×							
wardenensis sp. nov.		×	×												×		×	×	×											×	×		
wardenensis v. *quinquelata* nov.			×		×										×																		
oebisfeldensis Alberti																							×										
Thalassiphora pelagica Eis. & Gocht																													×	×	×	×	×
delicata sp. nov.	×		×	×		×	×		×	×	×		×	×		×			×	×	×		×	×	×	×	×	×	×	×	×	×	×

The occurrence of indigenous species of Dinoflagellate cysts in the London Clay

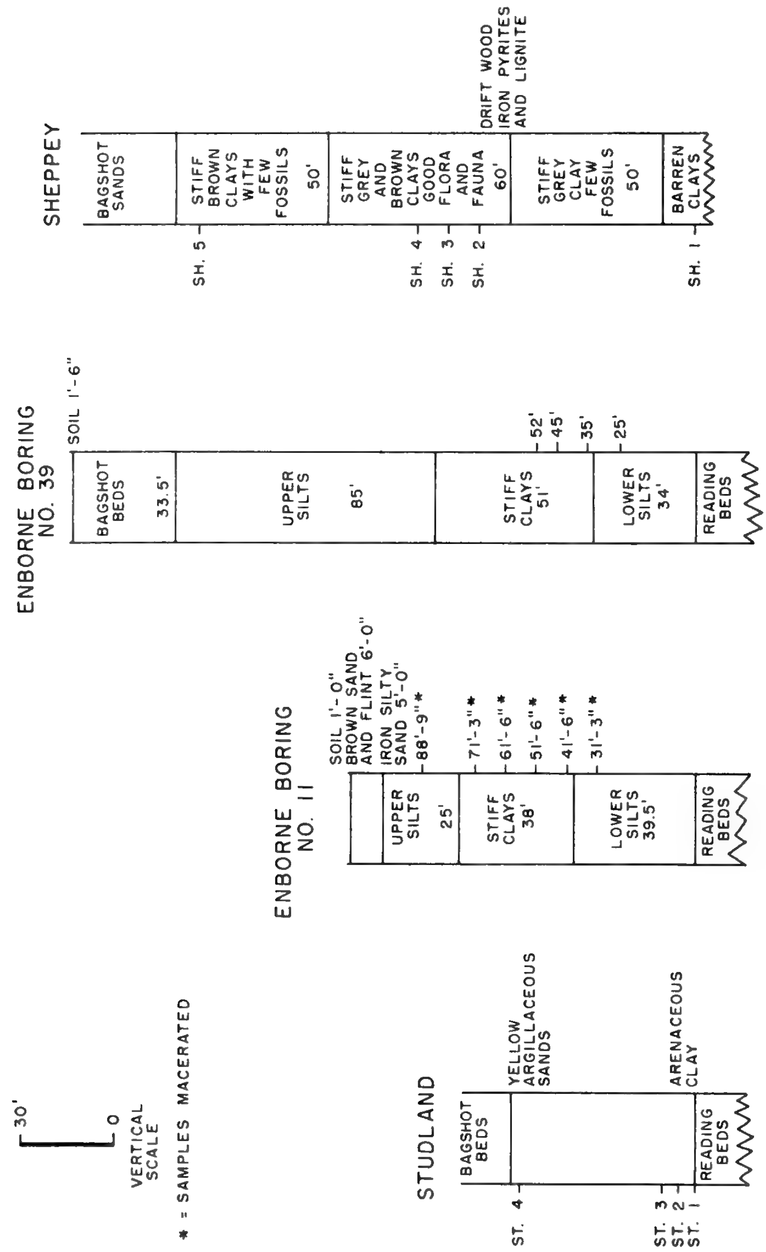


FIG. 7. The successions of the London Clay at Studland, Enborne and Sheppey showing the location of samples.

This uppermost division is represented at Sheppey by a continuation of the fourth division whose stiff clays with septaria come in 300–350 feet above the base. It is probable that most of the London Clay exposed at Sheppey falls within this (the fourth) division, the only possible exception being the " Foreshore Beds " of Davis (1936) which may mark the top of the third division. The first, second and most of the third divisions of Wrigley (1924) lying below the surface at Sheppey, only outcrop further east at Herne Bay and Reculver Bay, and are at present being investigated by Mr. A. Hussain in the Department of Geology at Sheffield University.

Davis recognized the following sequences in the Sheppey cliff section :

(d)	Stiff brown clays with few fossils	50′
(c)	Stiff grey and brown clays with good fauna and flora in lower part. Rarely *in situ*.	60′
(b)	Stiff blue clays. Few fossils.	50′
(a)	Foreshore. Barren clays, blue or lead coloured. . .	—

Group (a) The " Foreshore Beds ", probably include the upper parts of Wrigley's third division, whilst beds (b), (c) and (d) seem to belong to his fourth division, (d) including the Sheppey equivalent of Wrigley's division five. Samples have only been collected from groups (a), (c) and (d) because group (b) was never clearly exposed (Text-fig. 7).

IV. THE GENERA *HYSTRICHOSPHAERA* AND *ACHOMOSPHAERA*

By R. J. DAVEY & G. L. WILLIAMS

INTRODUCTION

The celebrated German microscopist, C. G. Ehrenberg, was the first to notice the occurrence of minute spiny organisms in flakes of Upper Cretaceous flint. These organisms were divided by him into two types. The first type possessed oval to polygonal shells bearing numerous forked processes and characterized by two furrows, one encircling the shell and the other perpendicular to it on one surface only. Such forms he recognized as belonging to a group of present-day plankton, the dinoflagellates. The second type had spherical or oval shells bearing forked processes as before but not possessing furrows. These forms he found rather difficult to identify, but came to the conclusion that they were silicified zygospores of a freshwater desmid known as *Xanthidium*. His initial findings were published in 1838 and 1843.

In 1838 Ehrenberg came to England and visited the Clapham Microscopical Society where he greatly influenced a group of British microscopists—Mantell, Reade, Deane, White and Wilkinson. Mantell (1845), after critically examining the shells of the *Xanthidia*, came to the conclusion that they were composed of some flexible substance, probably organic, perhaps chitin or cutin. Later (1850) he suggested that the spiny spheres were " probably the gemmules of sponges or other zoophytes ", and proposed the new genus *Spiniferites* to include them. This new name, however, was overlooked by subsequent workers and was eventually abandoned as a *nomen nudum* (Sarjeant 1964).

In 1904 the German marine biologist, Lohmann, after having worked on modern plankton and examined the fossil spiny spheres, decided that the latter were definitely planktonic. He came to the conclusion that they were eggs of a marine crustacean, probably a Copepod, and for this reason gave them the name *Ova hispida*. Reinsch (1905), for the first time, considered these fossils to be the cysts of marine algae, possibly dinoflagellates. He termed them " palinospheres ", another name which never came into general use.

O. Wetzel (1933) rejected all previous attributions and placed them in a new family, Hystrichosphaeridae, of unspecified systematic position. All the described species were included in his new genus *Hystrichosphaera*, and *Hystrichosphaera furcata* and *H. ramosa* were designated as joint type species.

Deflandre (1937) emended Wetzel's genus *Hystrichosphaera* to include only those forms possessing an equatorial girdle and polygonal fields. His choice of *H. furcata* as the sole type species has, however, proved an unfortunate one. Those forms without surface ornamentation he placed in a new genus, *Hystrichosphaeridium* Deflandre.

Evitt (1961) considered that *Hystrichosphaera* was not a motile dinoflagellate but a cyst possessing structures which are reflections of features seen in the motile stage. The presence of a precingular archaeopyle was noted and compared with that present

in *Gonyaulacysta* (Deflandre 1964). In 1963 he erected the genus *Achmosphaera* to accommodate species possessing a precingular archaeopyle and processes of the same form and distribution as found in the genus *Hystrichosphaera*, but lacking sutural crests or membranes.

Genus *HYSTRICHOSPHAERA* O. Wetzel 1933 : 33

1937. *Hystrichosphaera* O. Wetzel ; Deflandre : 61.

EMENDED DIAGNOSIS. Chorate to proximo-chorate cysts possessing a subspherical or ovoidal central body with a clearly defined reflected tabulation of 3–4′, 6″, 6c, 5‴, 0–1p, 1⁗, plate 6″ being generally reduced and triangular. Wall of central body composed of two layers, an inner endophragm and an outer periphragm. Cingulum always disposed in a laevo-rotatory spiral. Plate boundaries indicated by variably developed sutural crests or membranes, and gonal and sutural processes. Processes open or closed, solid or hollow, simple or branching. Length of processes variable, sometimes not extending beyond sutural crests, apical pole often marked by an elongate process. Archaeopyle precingular, formed by loss of reflected plate 3″.

TYPE SPECIES. *Xanthidium ramosa* Ehrenberg 1838. Upper Cretaceous (Senonian) ; Germany.

REMARKS. The generic diagnosis is emended to include reference to the reflected tabulation and to the presence of sutural processes in many species attributable to this genus.

The *Hystrichosphaera furcata–ramosa* complex

It is difficult to distinguish between *H. furcata* (Ehrenberg) and *H. ramosa* (Ehrenberg). The original drawings of Ehrenberg are inadequate for the present refined morphological studies and there is no description accompanying the figures of the types. The types for both species have either been lost or have not been re-examined recently, and many varied interpretations of the species have been made by later workers.

Ehrenberg (1838) figured a number of specimens as *Xanthidium furcatum* and *Xanthidium ramosum* without description or holotypes. His figures show that the main difference between the two species is the form of the extremities of the processes. *X. furcatum* has predominantly bifurcate processes ; only one of the figures (pl. 1, fig. 14*a*) shows trifurcate processes and then these do not predominate. *X. ramosum* has predominantly trifurcate processes and branching is shown to occur occasionally from a medial position on the processes. Branching is absent from Ehrenberg's figures of *X. furcatum*. The names given to the species confirm that Ehrenberg distinguished them on the type of process present.

White (1842) published the first account of both species. *X. furcatum* he described as having numerous, regularly arranged processes which gradually taper distally ;

thus they are not furcate. His figures are certainly not in accordance with those of Ehrenberg, and probably represent a different species. White's figures of *X. ramosum* closely resemble those of Ehrenberg for this species and are probably correct. The processes are predominantly trifurcate, often with a small bifurcation at their extremities.

X. ramosum had been figured earlier, without description, by Reade (1839) but his figure more closely resembles *X. complex* White than Ehrenberg's figures of *X. ramosum*. Ehrenberg (1854) refigured some of his specimens but again they were not accompanied by a text description.

O. Wetzel (1933) erected the genus *Hystrichosphaera* making both *H. furcata* and *H. ramosa* type species, this being contradictory to the rules of nomenclature. *H. furcata* is described as having strongly built processes with short bifurcations distally, each branch terminating in two spines. In *H. ramosa* some of the processes are divided into two, rarely more, they branch approximately half way along their length and finally divide into spinelets, usually three in number. The descriptions correspond with Ehrenberg's specimens, but O. Wetzel's plates are not distinct. Both species possess central bodies which are divided into fields or areas by sutures, from the junctions of which 6 to 30 processes arise. An equatorial girdle is often present. O. Wetzel considered *H. furcata* and *H. ramosa* to be varieties of the same species, and contrary to the rules of nomenclature, proposed a new name *H. communis* to contain them.

Deflandre (1935, 1936) figured a specimen of *H. furcata* which differs from Ehrenberg's types in that there is a proximal membrane and the majority of the processes have trifurcate extremities. Later (1937) he published the first account of the tabulation of *H. furcata* and also mentioned the well developed apical process. He pointed out that the processes invariably arose from nodal points at the junction of the plates. The processes are short and predominantly trifurcate, although some bifurcate processes do occasionally occur. The number of processes is approximately 30. The processes are not of equal length and tend to be shortest in the region of the triangular plate and longest at the poles. *H. ramosa* as figured by Deflandre differs from *H. furcata* only in the presence of processes which divide medially into two branches which themselves terminate distally in three spines. Like Wetzel Deflandre also considered *H. furcata* and *H. ramosa* to be varieties of one species, but suggested that the names *H. furcata* and *H. furcata* var. *ramosa* would be more appropriate, the latter being applied to individuals having slender and very divided processes. However the plates show only slight differences between the two types. Both possess bifurcate and trifurcate processes with medial branching and proximal membranes ; and considering the slenderness of the processes there is little or no difference. In fact both forms agree very well with *X. ramosum* of Ehrenberg.

Lejeune (1937) re-examined Ehrenberg's preparations and rediscovered one of his figured specimens (pl. 1, fig. 1) of *X. ramosum*. A detailed description of *H. ramosa* was given by Lejeune accompanied by some excellent figures. The majority of the

processes are trifurcate but some of the processes occupying a medial position are shown to be bifurcate. Some of the trifurcate processes possess small terminal bifurcations, and the membranes are always shown to be proximal. The number of processes is said to be approximately 40. Unfortunately, *H. furcata* was not similarly treated, Lejeune having apparently failed to recognize any of the original specimens figured by Ehrenberg as *Xanthidium furcatum* Ehrenberg.

Valensi (1955) described forms in which the processes terminate in two small spines or a fork. However his figures do not always correspond to the description given. Some of the processes are open with serrate lips and others are trifurcate with distal bifurcations. Some of the specimens have prominent crests with elevated membranes and differ from both of Ehrenberg's forms.

Eisenack (1958) described specimens attributed to *H. furcata* from the Aptian of Germany having short, thick processes with broad bases and dividing into two or three spines distally. In his description he emphasized the wide degree of variation in the species as interpreted by earlier workers.

Maier (1959) described and figured *H. furcata* from the Miocene of Germany, her forms possessing solid processes which divide distally in two to four spines. Gocht (1959) described specimens of *H. furcata* from the Neocomian of Germany as sometimes having isolated processes while others possessed well developed membranes along the plate boundaries uniting adjacent processes. *H. ramosa*, as described by Gerlach (1961), from the German Oligocene, possesses oval central bodies and trifurcate processes which are bifurcate distally.

Brosius (1963) restricted *H. furcata* to forms with bifurcate and trifurcate processes and *H. ramosa* to those with trifurcate processes, each furcation terminating in a short bifurcation. Cookson & Hughes (1964) had difficulty in identifying *H. ramosa* in the Albian/Cenomanian of Cambridge and distinguished it from *H. furcata* by its larger size, thicker-walled processes, more strongly outlined fields and more pronounced membranes.

Since the two species were first figured by Ehrenberg, there has been considerable difference of opinion as to how each species should be diagnosed, and subsequent authors appear to have attributed their specimens somewhat randomly to one, or more rarely, to both species. As Lejeune (1937) first pointed out with reference to these species in the Upper Cretaceous they, and closely related forms, form a continuous varying complex. One can treat such a complex in one of two ways. All described forms can be grouped under one species heading and varieties created or the group may be further subdivided, each new species being clearly defined. Detailed study of the Cenomanian and London Clay forms included within this complex rules out the adoption of the second alternative, since variation is so great as to render the interpretation of separate species, that would be of practical value, difficult if not impossible.

One of the specimens designated as *Xanthidium ramosum* by Ehrenberg (1838, pl. 1, fig. 15) was located by Lejeune (1937). This specimen (refigured in pl. 1, fig. 1) and another of Ehrenberg's preparations have been fully studied by one of the

authors (R.J.D.). The preparations, which are now in the Humboldt University, Berlin, were kindly lent for examination by Dr. K. Diebel whose assistance is gratefully acknowledged.

Specimens of *X. furcatum* as illustrated by Ehrenberg (1838, pl. 1, figs. 12, 14) cannot be traced and are either not distinctive enough for sure identification with his drawings or they have subsequently been lost. It is therefore proposed to treat the complex as one species to be designated *Hystrichosphaera ramosa*, since none of the specimens of *X. furcatum* as figured by Ehrenberg has been positively identified by later workers. The specimen figured by Ehrenberg (1838, pl. 1, fig. 15) is erected as the holotype of *H. ramosa* and the species is regarded here as the type species of the genus. Since Ehrenberg did not designate a holotype or give a description of *H. furcata*, and since later workers have failed to recognize it, it is proposed that forms attributed to *H. furcata* since 1933 be transferred to *H. ramosa* Ehrenberg.

Hystrichosphaera ramosa, in its revised acceptation, is an extremely long ranging species exhibiting a very considerable degree of variation in the detail of its morphology. Many of the extreme variants, encountered in isolation, would be considered sufficiently morphologically distinct from the typical forms to justify their erection as separate species ; but consideration of the whole assemblage shows all intermediate stages to be represented. However, our present knowledge of the species suggests that particular variational trends may have occurred only at certain stages within the total range of the species ; the extreme variants are capable of ready recognition and may prove of value as stratigraphical indices. A number of varieties are therefore here proposed, distinguished on the bases of process number and form, combined with character of the periphragm. Each represents the extreme development of a particular structure or combination of structures ; intermediate stages to the typical *H. ramosa* var. *ramosa* are in all cases known and are even frequent, so that differentiation of these forms at a higher taxonomic level is considered inappropriate.

Hystrichosphaera ramosa (Ehrenberg)

EMENDED DIAGNOSIS. A species of *Hystrichosphaera* possessing a thin walled central body, smooth, reticulate or granular. Gonal $\pm$ sutural processes always extending beyond confines of sutural crests, solid or hollow, the latter closed distally. Typical gonal processes trifurcate, sutural processes bifurcate, both commonly terminating distally in a small bifurcation.

HOLOTYPE. Slide "Feuerstein von Delitzsch, no. XXV" of Ehrenberg, Institut für Paläontologie und Museum der Humboldt Universität, Berlin. Upper Cretaceous ; Germany.

STRATIGRAPHICAL RANGE. This species has been recorded as *H. furcata* from the Oxfordian by Deflandre (1938) and Sarjeant (1960). Pleistocene examples have been observed by a number of workers, e.g. Fries (1951) and Rossignol (1964), and it has also been recorded from post-Pleistocene sediments dated 950 B.C. from West Wales. (Churchill & Sarjeant, in progress.)

Hystrichosphaera ramosa (Ehrenberg) var. ***ramosa*** nov.

Pl. 1, figs. 1, 6 ; Pl. 3, fig. 1; Text-fig. 8

1838. *Xanthidium ramosum* Ehrenberg, pl. 1, figs. 1, 2, 5.
1838. *Xanthidium furcatum* Ehrenberg, pl. 1, figs. 12, 14.
1854. *Xanthidium ramosum* Ehrenberg, pl. 7, figs. 9, 10.
1854. *Xanthidium furcatum* Ehrenberg, pl. 7, fig. 7.
1932. *Hystrichosphaera furcata* (Ehrenberg) O. Wetzel : 136.
1932. *Hystrichosphaera ramosa* (Ehrenberg) O. Wetzel : 144.
1935. *Hystrichosphaera furcata* (Ehr.) ; Deflandre : 14, pl. 5, fig. 9 ; pl. 8, fig. 3.
1936. *Hystrichosphaera furcata* (Ehr.) ; Deflandre : 62, text-fig. 108.
1937. *Hystrichosphaera furcata* (Ehr.) ; Deflandre : 61, pl. 11, figs. 1–3.
1937. *Hystrichosphaera ramosa* (Ehr.) ; Deflandre : 64, pl. 11, figs. 5, 7.
1937. *Hystrichosphaera ramosa* (Ehr.) ; Lejeune : 239, pl. 1, figs. 2–4 ; pl. 2, figs, 5–10.
1941. *Hystrichosphaera furcata* (Ehr.) ; Conrad, text-fig. 2, no. 1.
1947. *Hystrichosphaera furcata* (Ehr.) ; Deflandre : 22, text-fig. 1, no. 11.
1947. *Hystrichophaera ramosa* (Ehr.) ; Deflandre : 22, text-fig. 1, no. 13.
1952. *Hystrichosphaera furcata* (Ehr.) ; Deflandre, text-fig. 15.
1952. *Hystrichosphaera ramosa* (Ehr.) ; Deflandre, text-fig. 17.
1964. *Hystrichosphaera furcata* (Ehr.) ; Cookson & Hughes : 45, pl. 9, figs. 1, 2.

DIAGNOSIS. A variety of *H. ramosa* possessing an ovoidal central body bearing gonal and occasionally a small number of sutural processes. Gonal processes triangular in cross-section, sutural processes taeniate. Distally the processes are trifurcate or bifurcate often with bifid terminations, tapering to sub-conical in shape and sometimes branched. Sutural crests between processes proximal. Tabulation typical for genus.

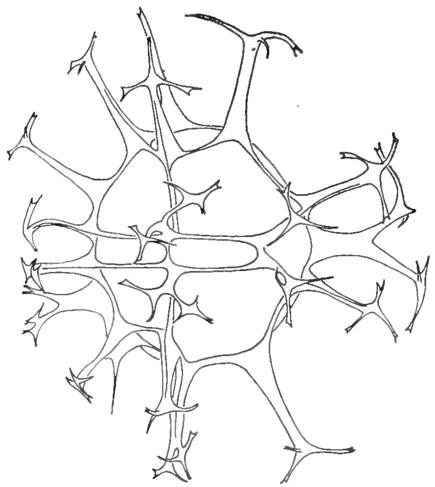


FIG. 8. *Hystrichosphaera ramosa* var. *ramosa* (Ehrenberg). The holotype, in lateral view. × c.700.

HOLOTYPE. Slide " Feuerstein von Delitzsch, no. XXV " of Ehrenberg (ringed in white on the third slice of flint). Lodged at the Institut für Paläontologie und Museum der Humboldt-Universität, Berlin. Upper Cretaceous ; Germany.

DIMENSIONS. Holotype : diameter of central body 42 by 48μ, length of processes 13–25μ. Range of Lower Cretaceous (Barremian) specimens : diameter of central body 34–41μ, length of processes 5–13μ. Number of specimens measured, 2. Range of Cenomanian specimens ; diameter of central body 30–50μ, length of processes 7–27μ. Number of specimens measured, 13. Range of London Clay (Ypresian) specimens ; diameter of central body 32–56μ, length of processes 11–20μ. Number of specimens measured, 9.

DESCRIPTION. The plates of the cingulum are distinctive, being elongate and six-sided. There are two gonal processes between adjacent cingular plates and these are usually connected by a well developed membrane. The longitudinal furrow is obvious and is considerably larger on the hypotract. A distinctive simple apical process is commonly present. When the trapezoid precingular archaeopyle is present it is noticeable that the margin appears to lie just within the boundary of plate 3″. One specimen of *H. ramosa* var. *ramosa* (Pl. 3, fig. 1) has been observed in the Upper Oxfordian (Throstler Clay, Upper Calcareous Grit) of England (Sarjeant 1960). The specimen is large (central body diameter 58 by 61μ, length of processes up to 19μ) but otherwise appears to be typical of this variety.

This variety has a known stratigraphic range from the Middle Barremian to the Ypresian.

REMARKS. *H. ramosa* var. *ramosa* is characterized by the form of its processes and the absence or scarcity of sutural processes. Doubtful descriptions or illustrations of forms classified as *H. furcata* or *H. ramosa* have not been included in the synonymy of *H. ramosa* var. *ramosa* and are placed in *H. ramosa* (Ehrenberg) var. indet. The varieties of *H. furcata* described by Rossignol (1964) must be transferred to *H. ramosa*.

Hystrichosphaera ramosa var. ***gracilis*** nov.

Pl. 1, fig. 5 ; Pl. 5, fig. 6

1955. *Hystrichosphaera ramosa* (Ehr.) ; Deflandre & Cookson : 263, pl. 5, fig. 8.
1963. *Hystrichosphaera ramosa* (Ehr.) ; Górka : 48, pl. 6, figs. 6, 7.

DERIVATION OF NAME. Latin, *gracilis*, slender or graceful—with reference to the slender, rather delicate processes.

DIAGNOSIS. A variety of *H. ramosa* (Ehrenberg) with smooth, thin-walled central body bearing gonal and sutural processes. Processes solid or hollow and relatively long and slender. Crests proximal and extending along all processes often as far as the trifurcation. Gonal processes mainly trifurcate, sutural processes bifurcate, all but smallest terminating with small trifurcation.

HOLOTYPE. B.M.(N.H.) slide V.51757(1). 5 feet above the base of London Clay ; Sheppey, Kent.

DIMENSIONS. Holotype : diameter of central body 35 by 43μ, length of processes 17–23μ. Range of London Clay specimens ; diameter of central body 32–61·5μ, length of processes up to 29μ. Number of specimens measured, 7. Range of Cenomanian specimens ; diameter of central body 28–33μ, length of processes up to 20μ. Number of specimens measured, 3.

REMARKS. *H. ramosa* var. *gracilis* is characterized by the slender, relatively long, gonal and sutural processes. The position of the sutural processes in the examples studied appears to be haphazard.

The known stratigraphic range of this variety is from the Cenomanian (England) to the Miocene (Australia).

Hystrichosphaera ramosa var. ***granosa*** nov.

Pl. 4, fig. 9

DERIVATION OF NAME. Latin, *granosus*, granular—with reference to the granular nature of the surface of the central body.

DIAGNOSIS. A variety of *H. ramosa* (Ehrenberg) similar to *H. ramosa* var. *gracilis* except that the surface of the central body is coarsely granular. Height of granules ranging up to 0·5μ.

HOLOTYPE. B.M.(N.H.) slide V.51752(2). 78 feet above the base of London Clay ; Sheppey, Kent.

DIMENSIONS. Holotype : diameter of central body 35 by 42μ, length of processes up to 19μ. Range : diameter of central body 33–45μ, length of processes up to 19μ. Number of specimens measured, 4.

REMARKS. A small number of specimens have been observed in the London Clay that apparently do not possess sutural processes. However, there is a complete gradation from these forms to those bearing many sutural processes and so separation solely on this characteristic was not thought to be practical.

H. ramosa var. *granosa* has only been recorded from the London Clay of England.

Hystrichosphaera ramosa var. ***multibrevis*** nov.

Pl. 1, fig. 4 ; Pl. 4, fig. 6 ; Text-fig. 9

1955. *Hystrichosphaera furcata* (Ehr.) ; Valensi : 586, pl. 4, fig. 4 ; pl. 5, fig. 12.
1958. *Hystrichosphaera furcata* (Ehr.) ; Eisenack : 406, pl. 25, figs. 4–8.

DERIVATION OF NAME. Latin, *multus*, much; *brevis*, short—with reference to the large number of short processes present in this variety.

DIAGNOSIS. A variety of *H. ramosa* (Ehrenberg) with smooth or slightly reticulate central body bearing short solid processes less than half the diameter of central body in length. Gonal processes trifurcate, sutural usually bifurcate, both types usually

terminating with a small bifurcation. Number and size of sutural processes varying considerably, up to three between adjacent gonal processes. Sutural crests proximal or well developed and always extending along gonal processes, making the latter subconical in shape. When the crests are well developed, the sutural processes may be reduced to delicate protuberances emanating from the crest border.

HOLOTYPE. B.M.(N.H.) slide V.51981(1). Metropolitan Water Board Borehole No. 11 at 63 feet depth, London Clay ; Enborne, Berkshire.

DIMENSIONS. Holotype : diameter of central body 35 by 44·5μ, length of processes up to 14μ. Range of London Clay specimens ; diameter of central body 35–59μ, length of processes up to 16μ. Number of specimens measured, 6. Range of Hauterivian and Barremian specimens ; diameter of central body 34–47μ. Length of processes up to 12μ. Number of specimens measured, 7. Range of Cenomanian specimens ; diameter of central body 31–46μ, length of processes up to 19μ. Number of specimens measured, 11.

REMARKS. *H. ramosa* var. *multibrevis* is characterized by the presence of short gonal and sutural processes. Examples from the Lower Cretaceous possess very short, rather rudimentary processes and differ from *H. dentata* (Gocht 1959) in having the characteristic tabulation of the genus which is lacking in Gocht's species. In the Cenomanian the processes are better developed but rather variable in form,

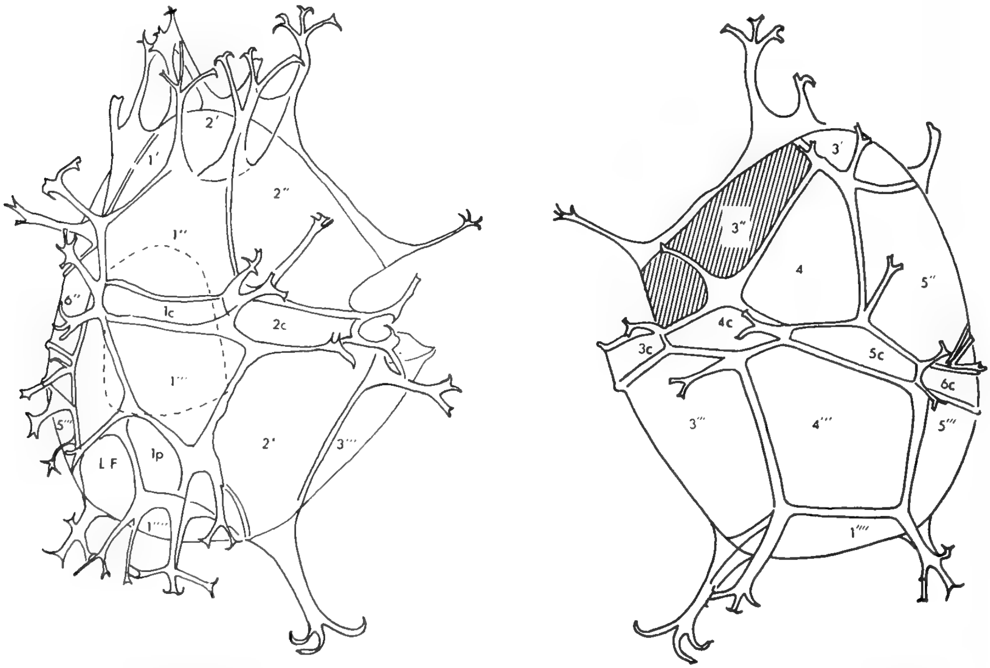


FIG. 9. *Hystrichosphaera ramosa* var. *multibrevis* nov. A specimen from the London Clay. Left, ventral view. Plate 3'' (the operculum of the archaeopyle) lies within the central body. Right, dorsal view. × c.1500.

stability being reached in the Eocene when the processes resemble those found in *H. ramosa* var. *ramosa* but are shorter and subconical, and considerably more numerous. *H. ramosa* var. *multibrevis* is similar to *H. furcata* var. *multiplicata* (Rossignol 1964) from the Pleistocene of the Eastern Mediterranean except for the absence of the two distinctive large dorsal antapical processes.

H. ramosa var. *multibrevis* has been recorded from the Lower Cretaceous (Hauterivian) to the Eocene (Ypresian) in England, from the Upper Cretaceous of France and from the Aptian of Germany.

Hystrichosphaera ramosa var. *membranacea* (Rossignol)

Pl. 4, figs. 8, 12

1964. *Hystrichosphaera furcata* var. *membranacea* Rossignol : 86, pl. 1, figs. 4, 9, 10 ; pl. 3, figs. 7, 12.

MATERIAL (Figured). B.M.(N.H.) slide V.51747(2). Metropolitan Water Board Borehole No. 11 at 53 feet depth, London Clay ; Enborne, Berkshire. Micropal. Lab., Sheffield University No. SL5. 173 ft. above base of London Clay ; Sheppey, Kent.

DIMENSIONS. V.51747(2) : diameter of central body 38·5 by 43μ, length of processes up to 19μ. Observed range : diameter of central body 31·5–45μ, length of processes up to 26μ. Number of specimens measured, 5.

REMARKS. The specimens belonging to this variety found in the London Clay agree fairly well with those observed by Rossignol (1964) from the Pleistocene. *H. ramosa* var. *membranacea* possesses a smooth walled central body with well developed membranes on the plate boundaries. The membranes are variable in height and development and may unite all or only few of the processes. However the membranes are commonly well developed only in the cingular and polar regions. The two large dorsal antapical processes noted by Rossignol are not noticeable in the Eocene forms.

The often extensive development of a membrane in the equatorial zone restricted to one side gives some of the specimens a superficial resemblance to the form figured as *H. ramosa* by Lejeune (1937).

Hystrichosphaera ramosa var. *granomembranacea* nov.

Pl. 4, fig. 4

DERIVATION OF NAME. Latin, *granosus*, granular ; *membrana*, membrane—with reference to the granular membranes present in this variety.

DIAGNOSIS. A variety of *H. ramosa* (Ehrenberg) possessing a central body with a granular surface. Membranes well developed on plate boundaries particularly in cingular and polar regions.

HOLOTYPE. B.M.(N.H.) slide V.51982(1). 99 feet above base of London Clay; Sheppey, Kent.

DIMENSIONS. Holotype: diameter of central body 47 by 49μ, length of processes up to 20μ. Range: diameter of central body 41·5–56μ, length of processes up to 27μ.

REMARKS. This variety is similar to *H. ramosa* var. *membranacea* except that the surface of the central body is granular; it has only been recorded from the London Clay of England.

Hystrichosphaera ramosa var. ***reticulata*** nov.

Pl. 1, figs. 2, 3

DERIVATION OF NAME. Latin, *reticulatus*, net-like—with reference to the reticulate nature of the periphragm.

DIAGNOSIS. A variety of *H. ramosa* (Ehrenberg) with central body composed of thin smooth endophragm and reticulate periphragm. Gonal and occasionally sutural processes triangular, taeniate or subconical. Gonal processes trifurcate and suturals bifurcate, both types usually terminating distally with small bifurcation. Crests commonly reticulate, proximal except where they extend along processes.

HOLOTYPE. Geol. Surv. Colln., slide PF.3038(1). Lower Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey, at 750 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype: diameter of central body 36 by 42μ, length of processes up to 14μ. Range: diameter of central body 33–59μ, length of processes up to 17μ. Number of specimens measured, 13.

REMARKS. The processes, in the specimens possessing both gonal and sutural processes, are subconical. After further study these examples may be separated from the usual type of *H. ramosa* var. *reticulata* possessing only gonal processes. This variety is generally similar to *H. ramosa* var. *ramosa* but is readily distinguished by the reticulate surface of the central body.

H. ramosa var. *reticulata* is present in small numbers throughout the Cenomanian of England.

Hystrichosphaera cingulata (O. Wetzel)

Pl. 1, fig. 9

1933. *Cymatiosphaera cingulata* O. Wetzel: 28, pl. 4, fig. 10.
1954. *Hystrichosphaera cingulata* (O. Wetzel) Deflandre: 258.
1955. *Hystrichosphaera cingulata* (O. Wetzel); Deflandre & Cookson: 267, pl. 6, figs. 4, 5.
1963. *Hystrichosphaera cingulata* (O. Wetzel); Górka: 51, pl. 6, figs. 8–10.
1963. *Hystrichosphaera cingulata* (O. Wetzel); Baltes: 587, pl. 4, figs. 12–17.
1964. *Hystrichosphaera cingulata* (O. Wetzel); Rossignol: 87, text-fig. G.

DESCRIPTION. Examples of *H. cingulata* are common in the Cenomanian of England and are very similar to those described by Deflandre & Cookson (1955) and

Górka (1963). *H. cingulata* is characterized by well developed crests beyond which the gonal processes or thickenings do not protrude, the latter acting apparently only as supporting structures. The processes may be either simple or may terminate with a small bifurcation. The surface of the central body is smooth ; however the periphragm forming the crests may be slightly reticulate. The reflected tabulation is typical of the genus.

H. cingulata has a stratigraphic range from the Cenomanian (England) to the Pleistocene (Eastern Mediterranean).

MATERIAL (Figured). Geol. Surv. Colln., slide PF.3039(1). Lower Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey, at 730 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Figured specimen : diameter of central body 37 by 39μ, height of crests up to 13μ. Range of Cenomanian specimens : diameter of central body 26–48μ, height of crests up to 13μ. Number of specimens measured, 15.

Hystrichosphaera cingulata var. ***reticulata*** nov.

Pl. 1, fig. 10 ; Pl. 2, fig. 4

DERIVATION OF NAME. Latin, *reticulatus*, net-like—with reference to the reticulate nature of the periphragm.

DIAGNOSIS. A variety of *H. cingulata* with central body composed of smooth endophragm and strongly reticulate periphragm often somewhat thickened. Gonal " processes " not protruding above sutural crests, processes acting more or less as supporting structures for crests. Processes simple or terminating with small bifurcation.

HOLOTYPE. Geol. Surv. Colln., slide PF.3039(2). Lower Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey, at 730 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype : diameter of central body 40 by 55μ, height of crests up to 14μ. Range : diameter of central body 33–59μ, height of crests up to 17μ. Number of specimens measured, 12.

REMARKS. This variety strongly resembles *H. cingulata* (O. Wetzel) but the central body has a strongly reticulate surface. Górka (1963) states that many of the French examples of *H. cingulata* are lightly punctate and so may well belong to *H. cingulata* var. *reticulata*.

H. cingulata var. *reticulata* occurs infrequently in the Middle and Upper Cenomanian of England.

Hystrichosphaera crassimurata sp. nov.

Pl. 1, fig. 11

DERIVATION OF NAME. Latin, *crassus*, thick ; *murus*, wall—with reference to the extreme thickening of the central body periphragm.

DIAGNOSIS. A species of *Hystrichosphaera* with well developed crests. Gonal processes reduced to supports for crests. Periphragm of each reflected plate area smooth and extremely thickened. Reflected tabulation typical for genus.

HOLOTYPE. Geol. Surv. Colln., slide PF.3040(1). Lower Chalk. H.M. Geological Survey Borehole, Fetcham Mill, Surrey at 670 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype : diameter of central body 44 by 46μ, height of crests up to 14μ. Range : diameter of holotype 36–46μ, height of crests up to 14μ. Number of specimens measured, 4.

DESCRIPTION. Only gonal processes are present and these do not extend beyond the limits of the crests. The processes are usually simple but may terminate in a small bifurcation. The periphragm of the crests is typically slightly granular whereas that of the central body is always smooth. The thickened periphragm on the central body may be up to 3·5μ thick.

This is a rare species, recorded only from the Middle and Upper Cenomanian of England.

REMARKS. High crests enclosing the processes are present in two other species of *Hystrichosphaera* : *H. cingulata* (Wetzel) and *H. pterota* (= *Cymatiosphaera pterota* Cookson & Eisenack). However *H. crassimurata* sp. nov. is readily distinguishable from these two species by the thickened areas of the periphragm on the central body.

Hystrichosphaera crassipellis Deflandre & Cookson

Pl. 1, figs. 7, 8

1954. *Hystrichosphaera crassipellis* Deflandre & Cookson, text-fig. 5.
1955. *Hystrichosphaera crassipellis* Deflandre & Cookson ; Deflandre & Cookson : 265, pl. 6, figs. 2, 3 ; text-fig. 20.
1961. *Hystrichosphaera crassipellis* Deflandre & Cookson ; Gerlach : 177, pl. 27, fig. 5 ; text-figs. 16–18.

DESCRIPTION. *H. crassipellis* possesses a thick central body wall (up to 6·5μ in thickness) which is coarsely reticulate. The reticulation is rather irregular having from almost circular to polygonal fields. The processes are gonal, subconical in shape and commonly bifurcate with bifurcating extremities. The paired cingular processes are joined by a membrane. The crests are proximal, reasonably well developed and may be reticulate, especially at their outer edges. *H. crassipellis* is a rare species occurring throughout the Cenomanian of England.

MATERIAL (Figured). Geol. Surv. Colln., slide PF.3033(2). Lower Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey, at 730 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Figured specimen : diameter of central body 45 by 46μ, length of processes 12–15μ, overall diameter 64–67μ. Range of Cenomanian specimens :

diameter of central body 34–68μ, length of processes up to 26μ. Number of specimens measured, 16.

REMARKS. The Cenomanian specimens greatly resemble those of Deflandre & Cookson (1954, 1955) from the Lower Eocene of Australia, except that they are smaller. *H. crassipellis* as illustrated by Maier (1959) is very different and cannot be included within this species.

Hystrichosphaera perforata sp. nov.

Pl. 5, fig. 7

DERIVATION OF NAME. Latin, *perforatus*, perforated—with reference to the perforate distal margins of the processes.

DIAGNOSIS. A species of *Hystrichosphaera* with smooth surfaced central body bearing both gonal and sutural processes. Processes either tri- or tetra-linguate, cylindrical and open with net-like perforations distally, or taeniate, being bi- or trifurcate distally. Medial branching of processes may occur. Tabulation typical of genus with plate 6″ having a triangular outline.

HOLOTYPE. B.M.(N.H.) slide V.51983(1). 85 feet above base of London Clay; Sheppey, Kent.

DIMENSIONS. Holotype: diameter of central body 40·5 by 50, length of processes up to 26μ. Range: diameter of central body 28–50μ, length of processes 15–26μ. Number of specimens measured, 4.

DESCRIPTION. *H. perforata* sp. nov. is characterized by two types of processes: (1) gonal processes being open, cylindrical with tri- or tetra-linguate margins and possessing a triangular cross-section, and (2) taeniate processes being sutural in position. The processes are united by proximal membranes, of varying height, often with serrate edges, running along the plate boundaries. The open gonal processes are strongly fenestrate distally on the secae and occasionally along their length. A few of the processes are similar to those of *H. ramosa* var. *ramosa* in being closed distally. Each seca is usually distally bifid. The sutural processes are perforate distally where they bi- or trifurcate, and sometimes medially.

REMARKS. Two specimens of *H. ramosa* which were recorded by Gerlach (1961) possessed processes perforate distally and along their length. All the processes of these two specimens are, however, closed and the perforations are in the form of small circular holes and not net-like as in *H. perforata*. *H. porosa* (Manum & Cookson 1964) from the Upper Cretaceous of Canada possesses similar, but shorter and broader, perforate processes and a characteristic reflected tabulation—1′, 5″, 5c, 5‴, 1⁗.

Hystrichosphaera buccina sp. nov.

Pl. 4, fig. 1 ; Text-figs. 10, 11

DERIVATION OF NAME. Latin, *buccina*, trumpet—with reference to the shape of the processes.

DIAGNOSIS. A species of *Hystrichosphaera* with central body composed of thick endophragm and thinner periphragm, the latter giving rise to gonal processes and

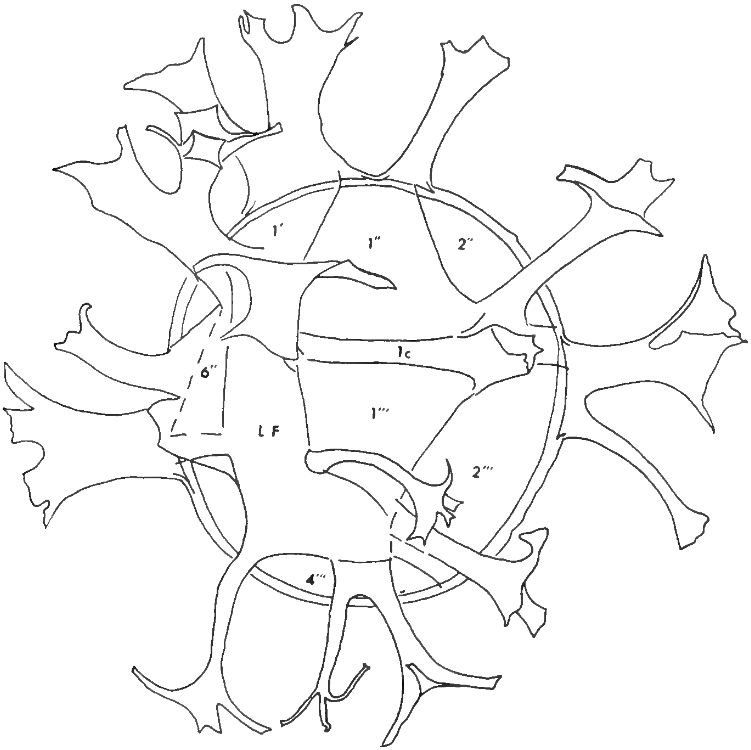


FIG. 10. *Hystrichosphaera buccina* sp. nov. Holotype, ventral view. × c.1000.

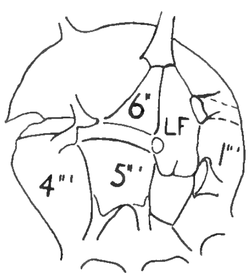


FIG. 11. *Hystrichosphaera buccina* sp. nov. A specimen from the London Clay, ventral view. × c.1000.

proximal crests. Surface of central body slightly granular or rarely reticulate. Processes only gonal, simple or branched, and always open distally. Reflected tabulation is 3–4′, 6″, 6c, 5‴, 1⁗.

HOLOTYPE. B.M.(N.H.), slide V.51989(1). 106 feet above base of London Clay ; Whitecliff Bay, Isle of Wight.

DIMENSIONS. Holotype : diameter of central body 58 by 62μ, length of processes up to 32μ. Range : diameter of central body 54–68μ, length of processes 24–36μ. Number of specimens measured, 4.

DESCRIPTION. The endophragm of the central body is 1·5–2μ thick and the periphragm up to 1μ. The processes terminate distally in three or more secae, which may be patulate, flaring or recurved. The tips of the secae may be oblate, bifid or bifurcate. This species occurs throughout the London Clay of England.

REMARKS. *H. buccina* sp. nov. is distinguished from all other species of *Hystrichosphaera*, except *H. tertiaria* (Eisenack & Gocht), by the characteristic form of the processes. *H. buccina* differs from *H. tertiaria* in the tabulation, the latter reflecting 5 precingular and 5 postcingular plates, 4 elongate rhombohedral cingular plates and a fifth triangular cingular plate. In *H. buccina* 6″ is reflected and is triangular, whilst 6c runs along its antapical edge. Often the boundary between 6″ and 6c is ill-defined and may only be seen at high magnification. *H. tertiaria* has only three apical plates whereas *H. buccina* may have 3 or 4. When 4 are present 1′ and 4′ are both narrow elongate plates and are in line with the corresponding shortened sulcus. The processes of one of the London Clay specimens are reticulate or occasionally perforate, but their form is different from that of *H. perforata* sp. nov.

Hystrichosphaera cornuta Gerlach

Pl. 4, fig. 7 ; Text-fig. 12

1961. *Hystrichosphaera cornuta* Gerlach : 180, pl. 27, figs. 10–12.

DESCRIPTION. The specimens are identical to those described by Gerlach (1961) and possess the following reflected tabulation—3–4′, 6″, 6c, 5‴, 1p, 1⁗, with plate 6″ triangular in outline. Whilst some species reflect only 3 apical plates, others show an elongate division of plate 1′ to give rise to two plates which are in line with the sulcus. There is occasionally an apical bulge which interrupts the otherwise regular outline of the central body and lies immediately below the apical process. Gonal and sutural processes are present, and may occasionally be open. In some individuals the large apical process possesses small lateral spines.

H. cornuta has only previously been recorded from the Middle Oligocene–Middle Miocene of N.W. Germany by Gerlach (1961).

MATERIAL (figured). B.M.(N.H.) slide V.51741(2). 85 feet above base of London Clay ; Sheppey, Kent.

DIMENSIONS. Figured specimen : diameter of central body 45 by 51μ, length of processes up to 11μ, length of apical process 25μ. Range : diameter of central body 39–52μ, length of processes 7–13μ, length of apical process 20–26μ. Number of specimens measured, 5.

Hystrichosphaera cornuta var. ***laevimura*** nov.

Pl. 4, fig. 5

DERIVATION OF NAME. Latin, *laevis*, smooth ; *murus*, wall—with reference to the smooth wall possessed by the central body in this variety.

DIAGNOSIS. A variety of *H. cornuta* (Gerlach) with smooth surfaced central body. Gonal and sutural processes short and subconical. A large distinctive apical process present often bearing small lateral spines.

HOLOTYPE. B.M.(N.H.) slide V.51752(3). 78 feet above base of London Clay ; Sheppey, Kent.

DIMENSIONS. Holotype : diameter of central body 43 by 53μ, length of processes up to 12μ. Range : diameter of central body 34–64μ, length of processes up to 14μ, length of apical process 16–32μ. Number of specimens measured, 4.

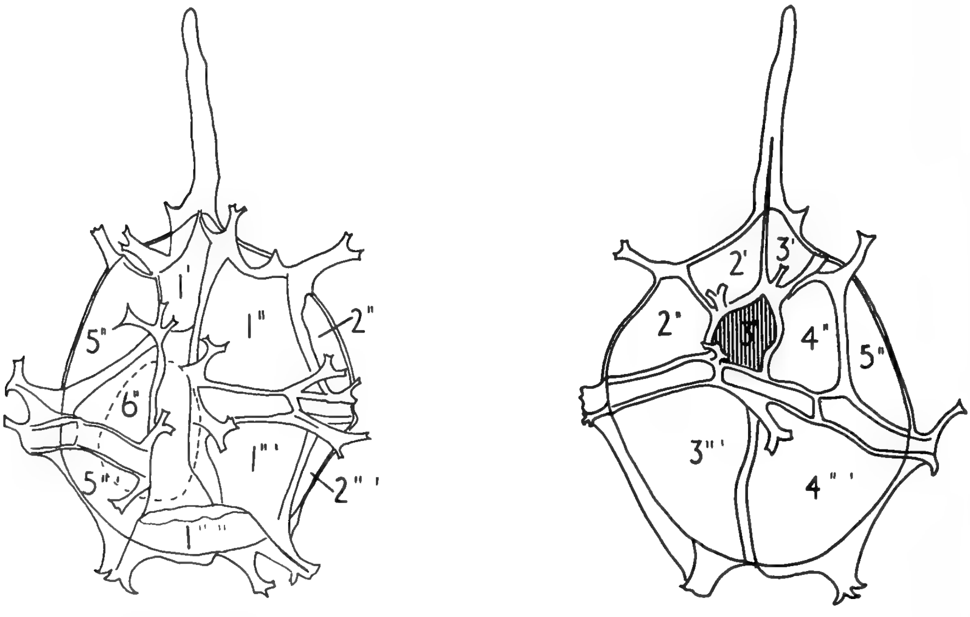


FIG. 12. *Hystrichosphaera cornuta* Gerlach. A specimen from the London Clay. Left, ventral view, plate 3″ (the operculum of the archaeopyle) lying within the central body ; right, dorsal view. × c.1000.

REMARKS. *H. cornuta* var. *laevimura* nov. differs from *H. cornuta* by possessing a central body with a smooth wall and is separated from this species because of the absence of intermediate forms with slightly granular walls. The apical bulge, occasionally found in *H. cornuta*, is also found in this variety. The processes of the latter are often more slender than those of *H. cornuta* but this feature is not characteristic.

This is a rare form, only recorded from the London Clay of England.

Hystrichosphaera cf. ***cornuta*** Gerlach

DESCRIPTION. The central body of this form is slightly granular and bears very short gonal and sutural processes. The processes may be simple, bifurcate or trifurcate. A moderate sized apical process is present.

MATERIAL. B.M.(N.H.) slide V.51985(1). 25 feet above base of London Clay ; Whitecliff Bay, Isle of Wight.

DIMENSIONS. V.51985(1) : diameter of central body 53 by 55μ, length of processes up to 9μ, length of apical process 18μ. Range : diameter of central body 31–55μ, length of processes 4–9μ, length of apical process 11–18μ. Number of specimens measured, 3.

REMARKS. *H.* cf. *cornuta* from the London Clay appears to be transitional to *H. speciosa* (Deflandre 1934). The central body is less granular and the processes, particularly the apical one, are shorter than is normal in *H. cornuta*. The apical process, however, is similar in structure.

Hystrichosphaera monilis sp. nov.

Pl. 5, fig. 2

DERIVATION OF NAME. Latin, *monile*, necklace or string of beads—with reference to the appearance of the sutural crests.

DIAGNOSIS. A species of *Hystrichosphaera* possessing a spherical central body with slightly granular surface. Processes short, sub-conical to cylindrical, closed, simple or distally forked. Granules concentrated along proximal sutural crests.

HOLOTYPE. B.M.(N.H.), slide V.51986(1). 78 feet above base of London Clay ; Sheppey, Kent.

DIMENSIONS. Holotype : diameter of central body 36 by 38μ, length of processes up to 11μ. Range : diameter of central body 31–46μ, length of processes up to 11μ. Number of specimens measured, 5.

DESCRIPTION. Distally the processes may be simple, bi- tri- or tetrafurcate. When the processes are furcate, the furcations are digitate and always erect. Each taeniate furcation may be bifid or have a serrate or entire distal margin. Some of the processes are fenestrate proximally.

REMARKS. The concentration of granules along the plate boundaries, the spherical shape of the central body and the short erect processes differentiate *H. monilis* sp. nov. from all other described species of *Hystrichosphaera*.

Hystrichosphaera sp.

Pl. 9, fig. 9

DESCRIPTION. A type of *Hystrichosphaera* with coarsely reticulate periphragm forming crests and processes, as well as surface of central body. The crests are well developed and bear small protruberances or stunted processes which terminate bluntly or are bifid. Gonal and a small number of sutural processes are present.

MATERIAL (figured). B.M.(N.H.), slide V.51724(1). Speeton Clay, Shell West Heslerton Borehole at 42·5 metres depth, West Heslerton, Yorkshire. Lower Cretaceous (Lower Barremian).

DIMENSIONS. Figured specimen : diameter of central body 39 by 39μ, length of processes up to 11μ. Second specimen : diameter of central body 43 by 51μ, length of processes up to 10μ.

REMARKS. This form has been encountered only rarely at one horizon, and it is characterized by its coarsely reticulate periphragm. It differs from *H. ramosa* in the reduced state of the processes and from *H. cingulata* var. *reticulata* in the presence of the latter. Since only two specimens were available for study and the presence of the typical *Hystrichosphaera* reflected tabulation was not verified. No specific name has been given.

Genus ***ACHOMOSPHAERA*** Evitt 1963 : 163

DIAGNOSIS. Test consisting of spherical to ellipsoidal central body with precingular archaeopyle and furcate, spine-like processes like those of *Hystrichosphaera* in both structure and distribution, but without sutural ridges or septa connecting their bases as in that genus. Tips of processes not connected. Wall two-layered ; layers typically in close contact between bases of processes.

TYPE SPECIES. *Hystrichosphaeridium ramuliferum* Deflandre 1937.

REMARKS. One of the authors (R. J. D.) was allowed, by kind permission of Professor Deflandre, to examine the type material. One paratype, figured by Deflandre (1937, pl. 14, fig. 6), under high magnification was seen to possess very faint lines on the surface of the central body delimiting the plate boundaries. Such lines were not observed on the holotype but this was probably due to the obscuring nature of particles within the flint. These faint lines, slight thickenings of the periphragm and comparable to the sutural crests of *Hystrichosphaera*, have been observed in a number of chemically prepared specimens belonging to this genus.

TABLE 2

Species and varieties of *Hystrichosphaera*	Surface of central body	Position of processes	Type of processes	Other characteristic features	Stratigraphic range
H. ramosa var. *ramosa*	Smooth	Gonal ± sutural	Tapering to subconical	Proximal crests	Upper Jurassic–Eocene (Oxfordian–Ypresian)
var. *multibrevis*	Smooth or slightly reticulate	Gonal & sutural	Subconical to rudimentary, commonly $<\frac{1}{2}$ central body diameter	Proximal crests, markedly extending up processes	Lower Cretaceous–Eocene (Hauterivian–Ypresian)
var. *reticulata*	Reticulate	Gonal ± sutural	Taeniate to subconical	Proximal crests	Upper Cretaceous (Cenomanian)
var. *gracilis*	Smooth	Gonal & sutural	Slender, commonly $>\frac{1}{2}$ central body diameter	Proximal crests	Upper Cretaceous (Cenomanian)–Miocene
var. *granulosa*	Granular	Gonal & sutural	Slender, commonly $>\frac{1}{2}$ central body diameter	Proximal crests	Eocene (Ypresian)
var. *grano-membranacea*	Granular	Gonal & sutural	Joined by membranes	Membranes commonly well developed in cingular regions	Eocene (Ypresian)
var. *membranacea*	Smooth	Gonal & sutural	Joined by membranes	Membranes commonly well developed in cingular and polar regions	Eocene–Pleistocene (Ypresian)
Hystrichosphaera sp.	Reticulate	Gonal & sutural	Processes rudimentary	Crests well developed. Processes are small protuberances	Upper Jurassic (Lower Barremian)

Species and varieties of *Hystrichosphaera*	Surface of central body	Position of processes	Type of processes	Other characteristic features	Stratigraphic range
H. cingulata var. *reticulata*	Reticulate	Gonal	Do not extend beyond crests	Periphragm sometimes thickened	Upper Cretaceous (Cenomanian)
H. crassimurata	Smooth	Gonal	Do not extend beyond crests	Periphragm greatly thickened within plate areas	Upper Cretaceous (Cenomanian)
H. crassipellis	Reticulate	Gonal	Subconical	Crests may be reticulate	Upper Cretaceous–Eocene (Cenomanian)
H. cingulata	Smooth	Gonal	Do not extend beyond crests	Crests well developed	Upper Cretaceous (Cenomanian)–Pleistocene
H. perforata	Smooth	Gonal & sutural	Taeniate or cylindrical	Open with net-like perforations distally	Eocene (Ypresian)
H. buccina	Smooth, slightly granular, or reticulate	Gonal	Cylindrical and open distally	Central body wall	Eocene (Ypresian)
H. cornuta	Granular	Gonal & sutural	Subconical	Large apical process	Eocene (Ypresian)–Middle Miocene
H. cornuta var. *laevimura*	Smooth	Gonal & sutural	Subconical	Large apical process	Eocene (Ypresian)
H. cf. *cornuta*	Slightly granular	Gonal & sutural	Simple to subconical	Short apical process	Eocene (Ypresian)
H. monilis	Slightly granular	Gonal & sutural	Subconical to cylindrical	Granules concentrated along sutural crests	Eocene (Ypresian)

The character and known distribution of species and varieties of the genus *Hystrichosphaera*

Achomosphaera ramulifera (Deflandre)

Pl. 2, fig. 3

1935. *Hystrichosphaera* cf. *ramosa* (Ehr.) ; Deflandre, pl. 5, fig. 11.
1937. *Hystrichosphaeridium ramuliferum* Deflandre : 74, pl. 14, figs. 5, 6 ; pl. 17, fig. 10.
1941. *Hystrichosphaeridium ramuliferum* Deflandre ; Conrad : 2, pl. 1, fig. J.
1948. *Hystrichosphaeridium ramuliferum* Deflandre ; Pastiels : 39, pl. 3, figs. 17–19.
?1952. *Hystrichosphaeridium ramuliferum* Deflandre ; W. Wetzel : 398, pl. A, fig. 9 ; text-fig. 9.
1952. *Hystrichosphaeridium ramuliferum* Deflandre ; Deflandre, text-fig. 4.
1955. *Hystrichosphaeridium ramuliferum* Deflandre ; Valensi : 594, pl. 4, fig. 6.
1959. *Hystrichosphaeridium ramuliferum* Deflandre ; Gocht : 71, pl. 3, fig. 9.
1963. *Hystrichosphaeridium ramuliferum* Deflandre ; Baltes : 586, pl. 7, figs. 13, 17, 18.
1963. *Hystrichosphaeridium ramuliferum* Deflandre ; Górka : 59, pl. 8, fig. 3 ; text-fig. 6, figs. 3, 4.
1963. *Baltisphaeridium ramuliferum* (Deflandre) Downie & Sarjeant : 92.
1963. *Achomosphaera ramulifera* (Deflandre) Evitt : 163.

DESCRIPTION. Representatives of this species occur infrequently in the Cenomanian of England and are very similar to the type material. The central body is smooth or very slightly reticulate and upon it may be traced lines marking the reflected plate boundaries. The processes are hollow, often possessing rather bulbous bases, and having usually trifurcate with bifurcating extremities. The cingular processes are commonly joined and a distinctive apical process is usually present. The London Clay forms attributed to *A. ramulifera* often differ from the type material in having processes with more than three furcations, exceptionally six spines arising from one process. When six spines are present, they have apparently resulted from the elongation of the bifid tips of the three original furcations. Pastiels (1948) also recorded forms from the Ypresian of Belgium which may have more than three spines arising from a single process. The surface of the central body may be smooth or slightly granular.

The species has a stratigraphic range from the Cenomanian to the Middle Miocene.

As with *Hystrichosphaera ramosa*, *A. ramulifera* is probably divisible into a number of varieties ; one obvious variety would be those forms possessing multifurcate processes as opposed to the trifurcate processes of the type material. In the present state of knowledge, however, it is better to proceed cautiously in the erection of varieties, since too few specimens have been studied for an adequate picture to have emerged.

DIMENSIONS. Cenomanian forms : diameter of central body 40–56μ, length of processes up to 36μ. Number of specimens measured, 4. London Clay forms : diameter of central body 24–54μ, length of processes up to 35μ. Number of specimens measured, 10.

Achomosphaera ramulifera var. ***perforata*** nov.

Pl. 5, figs. 1, 4

DERIVATION OF NAME. Latin, *perforatus*, perforated—with reference to the perforate nature of the processes.

DIAGNOSIS. A variety of *A. ramulifera* with gonal processes fenestrate proximally and sometimes distally.

HOLOTYPE. B.M.(N.H.) slide V.51764(1). 14 feet above base of London Clay ; Whitecliff Bay, Isle of Wight.

DIMENSIONS. Holotype : diameter of central body 33 by 42μ, length of processes 16–18μ. Range : diameter of central body 33–56μ, length of processes 15–26μ. Number of specimens measured, 3.

REMARKS. The forms placed in *A. ramulifera* var. *perforata* differ from the typical *A. ramulifera* by the presence of perforate processes. This characteristic was not thought distinctive enough to justify the creation of a new species.

This variety occurs infrequently in the London Clay (Ypresian) of England.

Achomosphaera alcicornu (Eisenack)

Pl. 5, fig. 3

1954. *Hystrichosphaeridium alcicornu* Eisenack : 65, pl. 10, figs. 1, 2 ; text-fig. 5.
1961. *Hystrichosphaeridium alcicornu* Eisenack : Gerlach : 188–189, pl. 28, fig. 7.

DESCRIPTION. The London Clay specimens are very similar to *H. tertiaria* (Eisenack & Gocht) and differ only in the absence of clearly defined plate boundaries. A precingular archaeopyle is present. That the archaeopyle is precingular is determined by its shape and the presence of 5 surrounding processes. The apical process and the cingular processes are typically branched. As in all species of *Achomosphaera* only gonal processes are present. The occasional specimen in the London Clay is slightly granular and some possess processes that are perforate distally.

MATERIAL (figured). B.M.(N.H.) slide V.51765(1). Metropolitan Water Board Borehole No. 11 at 83·25 feet depth. London Clay : Enborne, Berkshire.

DIMENSIONS. Figured specimen : diameter of central body 54 by 54μ, length of processes 28–40μ. Range : diameter of central body 49–66μ, length of processes 24–46μ. Number of specimens measured, 4.

REMARKS. The stratigraphic range of *A. alcicornu* is from the Eocene (Ypresian) to the Middle Miocene (Gerlach 1961).

Achomosphaera sagena sp. nov.

Pl. 2, figs. 1, 2

DERIVATION OF NAME. Latin, *sagena*, fish-net—with reference to the distinctive net-like pattern on the surface of the central body.

DIAGNOSIS. Wall of central body extremely thick, apparently composed of columar elements, surface coarsely reticulate. Closed gonal processes hollow, trifurcate with bifurcate extremities, and commonly possessing reticulate bases. Processes sometimes branched, branding mainly confined to cingular zone. Characteristically shaped precingular archaeopyle often present.

HOLOTYPE. Geol. Surv. Colln. slide PF.3041(1). Lower Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey, at 650 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype : diameter of central body 48μ, length of processes up to 20μ. Range : diameter of central body 35–59μ, length of processes up to 28μ. Number of specimens measured, 8.

DESCRIPTION. The wall of the central body, which may be up to 5μ thick, is composed of elongate cellular elements lying perpendicular to the surface. The surface reticulation is coarse and may be up to 1·5μ across (Pl. 2, fig. 2).

A. sagena sp. nov. has only been recorded from the Cenomanian of England.

REMARKS. *A. sagena* is similar to *H. crassipellis* (Deflandre & Cookson) in that both possess thick walls of an identical nature with a reticulate surface. However sutural crests are absent in *A. sagena*.

Achomosphaera neptuni (Eisenack)

Pl. 3, fig. 7 ; Pl. 9, fig. 11

1958. *Baltisphaeridium neptuni* Eisenack : 399, pl. 26, figs. 7, 8 ; text-fig. 8.
1959. *Baltisphaeridium neptuni* Eisenack ; Gocht : 73, pl. 4, fig. 14

DESCRIPTION. *A. neptuni* possesses a central body with a reticulate or sometimes slightly fibrous surface. The processes are gonal in position, taeniate or taeniate-triangular and may be bifurcate or trifurcate. In the cingular zone the processes are branched. The processes are fibrous, the fibres sometimes radiating from the bases of the processes and these may be slightly thickened along the reflected plate boundaries joining the processes. A precingular archaeopyle is often present.

MATERIAL (figured). B.M.(N.H.) slides V.51716–17. Speeton Clay, Shell West Heslerton boring at 103·25 metres depth, West Heslerton, Yorkshire. Lower Cretaceous (Middle Hauterivian).

DIMENSIONS. V.51716, diameter of central body 61 by 66μ, length of processes up to 28μ. V.51717, diameter of central body 47 by 52μ, length of processes up to 21μ.

REMARKS. The Hauterivian examples strongly resemble those forms illustrated by Eisenack (1958) from the Aptian of Germany. In both of Eisenack's photographs (pl. 26, figs. 7 and 8) the views are either apical or antapical, a rather misleading orientation, the archaeopyle being seen in profile on the top side of these figures. The antapical view is shown in one of the specimens figured here, pl. 3, fig. 7, the archaeopyle being to the north-east. The processes of *A. neptuni* are very characteristic and it should be noted that they are not distally bifurcate as is usual in this genus and in *Hystrichosphaera*.

OTHER SPECIES

Achomosphaera hyperacantha (Deflandre & Cookson). This species, *Hystrichosphaera hyperacantha* Deflandre & Cookson 1955, which possesses very faint or invisible plate outlines is here considered to belong to the genus *Achomosphaera* Evitt and is renamed accordingly. Miocene ; Australia. *Achomosphaera triangulata* (Gerlach 1961 : 194, pl. 29, fig. 1) is here transferred to *Achomosphaera* on the basis of the possession of a precingular archaeopyle and the arrangement of the processes. Miocene ; Germany.

CONCLUSIONS

The characteristics and known stratigraphical distribution of the species and varieties of the genus *Hystrichosphaera* are summarized in the accompanying table (Table 2). The varieties of *H. ramosa*, as has been previously pointed out, are intergrading and, as one would expect, no clear stratigraphical picture emerges. The more distinctive species of this genus, when better known, may be of some stratigraphic value. For instance *H. crassipellis* (Deflandre & Cookson) has not been recorded from deposits earlier than the Cenomanian, nor has it been recorded from the Ypresian of England. Thus its stratigraphic range appears limited. Similarly *H. cornuta* (Gerlach) has not been recorded from deposits earlier than Tertiary.

Species of *Hystrichosphaera* are extremely rare in the Upper Jurassic, becoming more common in the Lower Cretaceous and from the Upper Cretaceous to the present day are an important constituent of the dinoflagellate cyst population. Variation has, however, been on a rather limited theme so making species differentiation extremely difficult. Moreover there appears to be a complicated plexus of evolution, particularly noticeable in the *H. ramosa* group. More detailed studies in the future may, however, throw light on some of these problems and aid the systematist and the stratigrapher.

V. THE GENUS *HYSTRICHOSPHAERIDIUM* AND ITS ALLIES

By R. J. DAVEY & G. L. WILLIAMS

INTRODUCTION

The early history of the study of fossil dinoflagellate cysts, first described by Ehrenberg (1838), is discussed in the previous chapter.

White (1842) was the first to describe the forms possessing tubular processes in his section on types of *Xanthidia tubifera*. In 1933, O. Wetzel placed all the then regarded species of fossil microplankton in the new genus *Hystrichosphaera*. Deflandre (1937) subdivided this genus separating those forms possessing an equatorial girdle and polygonal fields, which he placed in the genus *Hystrichosphaera* emend., and those without surface ornamentation which he placed in a new genus *Hystrichosphaeridium*. The diagnosis of the genus *Hystrichosphaeridium* was given as follows : " This genus comprises all the hystrichospheres totally destitute of an equatorial system of elongate plates and whose shell, in general, does not bear fields or plates limited by sutures. The shell, of dimensions greater than 20μ, is most often spherical or spheroidal ; some species, however, are more or less elongate."

Eisenack (1958) emended and restricted this genus as follows : " Hystrichospheres with spherical to oval, non-tabulate central shell and with more or less numerous, mostly well separated and in general similar appendages, the ends being open and often expanded in funnel-like fashion." Those species not included in *Hystrichosphaeridium* by Eisenack have been revised by Downie & Sarjeant (1963).

Before classification of the spiny spheres placed in the genus *Hystrichosphaeridium* Deflandre could be attempted with any precision, their affinities had to be determined. Certain organisms such as forms belonging to the genus *Gonaulacysta*, are associated with species placed in *Hystrichosphaeridium*, and have a similar two layered body-wall apparently composed of the same or a very similar organic substance. These organisms are obviously related to the dinoflagellates and are either resting or reproductive cysts. They possess a characteristic ornamentation which can be related to the theca of modern dinoflagellates ; for example the crests marking the tabulation as seen in *Gonyaulacysta* and *Hystrichosphaera* or less obvious the distinctive equatorial region as possessed by *Deflandrea* or *Palaeohystrichophora*.

Thus many forms of fossil microplankton could definitely be said to be cysts of dinoflagellates, but what of the genus *Hystrichosphaeridium* ? Numerous forms had been attributed to this genus but dinoflagellate features had not been definitely noted in any of them. In fact they appeared to be simple spherical shells possessing a number of randomly arranged tubular appendages, usually with an opening or pylome of some kind which no doubt was used by the organisms as an exit. It was not until 1961 that Evitt pointed out the importance of these openings. He drew attention to the fact that most of the openings had angular margins and realized that here was evidence of breakage along a definite line. These openings, or " archaeo-

pyles " as he called them, were not irregular ruptures of a cyst wall but within a species were of constant shape and size. In forms that are definitely cysts of dinoflagellates, archaeopyles are formed by the loss of areas which correspond to a single plate or plates of the original dinoflagellate theca. Four types of archaeopyle were differentiated by Evitt. They are the precingular and intercalary archaeopyles, each formed by the loss of one plate ; the apical archaeopyle formed by the loss of the apical region, commonly four plates ; and the epitractal archaeopyle formed by the loss of the whole of the epitract above the girdle. Examination of species from the genus *Hystrichosphaeridium* reveals that the archaeopyle is practically always apical for three reasons :

(1) Surrounding the archaeopyle, in forms possessing less than 30 processes, there are constantly six processes corresponding to six precingular plates ;
(2) The detached operculum frequently bears four processes, reflecting the four apical plates found in many dinoflagellates ;
(3) In ovoidal or elongate forms the archaeopyle is usually formed at one of the extremities.

It was discovered in a number of forms, for instance *H. tubiferum* (Ehrenberg), that there was an obvious circular arrangement of the processes around the central body of the cyst, and that the number of processes was equal to the number of plates possessed by forms having a typical *Gonyaulax*-type tabulation. Thus in the above forms, one process on the central body of the cyst reflects one plate in the dinoflagellate theca, the process extending from the cyst to the centre of the plate. Such processes are referred to as being intratabular and from them may be calculated the original tabulation of the dinoflagellate.

Apart from the apical archaeopyle other features may be used in the orientation of the specimen and the elucidation of the process arrangement. Although the processes may all be of the same type, the sulcal processes, like the corresponding plates, are usually relatively small in size. The antapical process and the cingular processes usually expand to some extent and terminate with a spinous or serrate margin. The spines become finer away from the process margin and it is very easy to imagine a plate affixed to such a process termination.

All the above points seem to indicate conclusively that forms belonging to the genus *Hystrichosphaeridium* are cysts of dinoflagellates. The cysts are formed within dinoflagellate thecae, during or as a response to adverse conditions, the processes acting as pillars between the cyst and the thecal wall, and holding the cyst in position. Subsequently to the cyst formation the dinoflagellate theca is lost, the latter only very rarely being observed in preserved material. Sarjeant (1965, text-fig. 3) tentatively reconstructed the original tabulation of a dinoflagellate theca from the distribution of the processes for the species, *Oligosphaeridium vasiformum* (Plate 9, fig. 7).

Evitt (1961) suggests that there were three main divisions in the genus *Hystrichosphaeridium* : those forms possessing cingular or girdle processes of similar form to the other processes, those with distinct, often more slender, cingular processes and

those forms having a cingular region devoid of processes. He concludes that the character of the cingular processes, or their absence, is of taxonomic importance and could be used in the subdivision of this genus.

During a revision of the genus *Hystrichosphaeridium* it was noticed that most of the species could be placed in well-defined groups based primarily on the type of archaeopyle, the number of processes on the apical region and the overall number of processes on the central body. Forms possessing an apical archaeopyle and one process per plate may have either one, three or four apical processes, the familiar type of *Hystrichosphaeridium* possessing four apical processes. Subdivision of this group was made on the presence or absence and type of cingular process. The genus *Hystrichosphaeridium* is emended to restrict it to forms possessing normal tubular cingular and sulcal processes. These forms possess a process arrangement reflecting a certain tabulation, that is characterized by the type species *H. tubiferum* (Ehrenberg) $-4'(-5')$, $6''$, 6c, 5–$6'''$, 1p, $1''''$ and a variable number of sulcal processes. Forms where the cingular processes are absent are placed in a new genus *Oligosphaeridium*. A third genus, *Perisseiasphaeridium* gen. nov., is erected to contain forms somewhat intermediate between the previous two genera, possessing cingular and sulcal processes not of the normal tubular type, but smaller and usually closed.

The genus *Litosphaeridium* gen. nov., is characterized by the possession of three apical processes and the absence of cingular processes. Finally in this group possessing an apical archaeopyle and one process per plate is the genus *Cordonsphaeridium* (Eisenack) which is characterized by having an archaeopyle formed by the loss of a single apical plate.

Two new genera possessing an apical archaeopyle but more than one process per plate are erected. *Polysphaeridium* gen. nov., possesses numerous processes all of the same type (*Diphyes* is easily distinguishable by the presence of a large antapical process) and *Tanyosphaeridium* gen. nov. possesses an elongate central body and at the antapex probably 3 to 6 antapical processes.

Two new genera have been erected possessing an epitractal archaeopyle. *Homotryblium* gen. nov. possesses tubular processes of a more or less constant size, there being three apical processes. The presence of three apical processes may indicate a relationship with *Litosphaeridium* gen. nov., however cingular and sulcal processes are well developed in *Homotryblium* whereas in *Litosphaeridium* they are absent or very reduced. The other genus possessing an epitractal archaeopyle is *Callaiosphaeridium* gen. nov. which is represented by only one species, *C. asymmetricum* (Deflandre & Courteville). It is extremely distinctive, possessing both solid and tubular processes, one or perhaps two, apical processes and no antapical processes.

Genus ***HYSTRICHOSPHAERIDIUM*** Deflandre 1937 : 68

1958. *Hystrichosphaeridium* Deflandre ; Eisenack : 399, 400.

EMENDED DIAGNOSIS. Subspherical chorate cysts possessing a reflected tabulation of $4'$ $(-5')$, $6''$, 6c, 5–$6'''$, 1p, $1''''$ and a variable number of sulcal processes. Processes

hollow, open distally, intratabular, one process per plate area. Number of processes rarely exceeding 30. Archaeopyle apical.

TYPE SPECIES. *Xanthidium tubiferum* Ehrenberg 1838. Upper Cretaceous; Germany.

REMARKS. The central body is composed of two membranes, an inner endophragm and an outer periphragm, the latter also comprising the processes. In contrast to the genus *Oligosphaeridium*, the genus *Hystrichosphaeridium* posseses 6 cingular processes. The cavities of the processes are never in contact with the interior of the central body. The sulcal processes of this genus are often noticeably smaller than the other processes which are approximately of the same size, except for the antapical process which may be larger.

The above emendation restricts the genus *Hystrichosphaeridium* to those forms possessing the given tabulation and open processes. Other forms possessing open processes and formerly included in *Hystrichosphaeridium* have been placed in new genera according to the type of archaeopyle, the tabulation, the number and form of the processes and the shape of the central body.

Hystrichosphaeridium tubiferum (Ehrenberg)

Pl. 6, figs. 1, 2; Pl. 8, fig. 5; Pl. 10, fig. 2; Text-fig. 13

1838. *Xanthidium tubiferum* Ehrenberg, pl. 1, fig. 16.
1848. *Xanthidium tubiferum* Ehrenberg; Bronn: 1375, pl. 1, fig. 16.
1854. *Xanthidium tubiferum* Ehrenberg; Ehrenberg, pl. 7, fig. 48; pl. 37, fig. 7, no. 11.
1904. *Ovum hispidium* (*Xanthidium tubiferum*) Ehrenberg; Lohmann: 21.
1933. *Hystrichosphaera tubifera* (Ehrenberg) O. Wetzel: 40, pl. 4, fig. 16.
1937. *Hystrichosphaeridium tubiferum* (Ehrenberg) Deflandre: 68. (The specimens figured are of *H. recurvatum*.)
1940. *Hystrichosphaeridium tubiferum* (Ehrenberg); Lejeune-Carpentier: 218, figs. 1–4.
1941. *Hystrichosphaeridium tubiferum* (Ehrenberg); Conrad, pl. 1F, fig. 2F.
1952. *Hystrichosphaeridium tubiferum* (Ehrenberg); Gocht, pl. 1, fig. 4.
1963. *Hystrichosphaeridium tubiferum* (Ehrenberg); Górka: 55, pl. 8, figs. 1, 2; text-pl. 6, figs. 1, 2.

EMENDED DIAGNOSIS. Central body spherical to subspherical, smooth or slightly granular wall composed of two layers. Processes well developed, tubiform, open distally with entire or serrate circular margin. Processes give a reflected tabulation of 4–5′, 6″, 6c, 5–6‴, 1p, 1⁗ and a variable number of sulcal plates, commonly 4–5. Apical archaeopyle usually present.

HOLOTYPE. Slide XXV in a series of flints from Delitzsch, Institut für Paläontologie u. Museum der Humboldt-Universität, Berlin.

DIMENSIONS. Holotype: diameter of central body 33 by 34μ, length of processes 27–29μ, number of processes 24. Paratype: diameter of central body 33 by 36μ, length of processes 19–22μ.

Description. Central body composed of thin smooth endophragm and smooth or slightly granular periphragm, the latter also forming the processes. The processes are tubiform with distally a denticulate to serrate circular margin. At the base of each process is a characteristic circular mark caused by the initial divergence of the endophragm and periphragm. The processes, up to 30 in number, are usually shorter in length than the small diameter of the central body. They are of unequal width, the sulcal processes being finer and usually shorter. Lejeune-Carpentier (1940), after examination of the type material, records that this species is common from the Upper Turonian and Senonian.

The processes of the London Clay specimens often possess unusual foliaceous outgrowths emanating from the margin and these may be diagnostic enough to differentiate Eocene forms from Upper Cretaceous forms. All the London Clay forms have at least 20 processes. 10 specimens were measured, the diameter of the central body being 28–53µ and length of processes 13–29µ.

H. tubiferum is uncommon in the Cenomanian of Fetcham Mill (Surrey) and is rather variable in the form of its processes. Specimens which closely resemble the holotype have been observed, the sulcal processes, however, being less noticeably small. At the base of the Cenomanian the processes of *H. tubiferum* expand distally and terminate in a denticulate margin, a few short secae are often present. Towards the top of the Cenomanian the processes do not expand so much and the secae are more pronounced and isolated. Diameter of central body 30–51µ, length of processes 15–37µ, 26 specimens being measured.

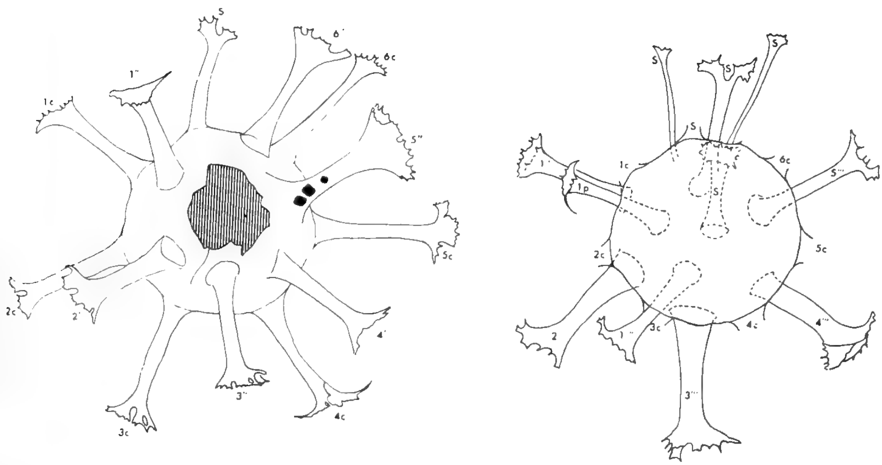


Fig. 13. *Hystrichosphaeridium tubiferum* (Ehrenberg). A specimen from the London Clay. Left, apical view showing the archaeopyle, precingular and cingular processes, and a single sulcal process ; right, antapical view (by transparency) showing the precingular, sulcal, posterior intercalary and antapical processes. × c. 1000.

Discussion. *H. tubiferum* has been recorded many times but often incorrectly. The specimens figured by Reade (1839, pl. 9, figs. 6, 19) and Deflandre (1937, pl. 12, fig. 14; pl. 13, figs. 2, 14) show all the characteristics of *Hystrichosphaeridium recurvatum* (White) and should be regarded as attributable to this species. *H. tubiferum* (Valensi, 1955, pl. 4, fig. 2; pl. 5, fig. 8) may also belong to *H. recurvatum*.

The specimens illustrated by Eisenack (1958, pl. 25, fig. 16) and Pocock (1962, pl. 15, fig. 230) should probably be referred to *Oligosphaeridium complex* (White).

A number of other specimens have been referred to *H. tubiferum* but their true systematic position is doubtful, and almost certainly they do not belong to this species.

Hystrichosphaeridium tubiferum (Ehrenberg) var. ***brevispinum*** nov.

Pl. 10, fig. 10

Derivation of name. Latin, *brevis*, short; *spina*, spine—referring to the short processes.

Diagnosis. A variety of *Hystrichosphaeridium tubiferum* with processes rarely exceeding one-third of the diameter of the central body.

Holotype. B.M.(N.H.) slide V.51738(1). Metropolitan Water Board Borehole No. 39, at 160 feet depth, London Clay; Enborne, Berkshire.

Dimensions. Holotype: diameter of central body 32 by 36μ; length of processes up to 11μ; width of processes up to 11μ; number of processes 23. Range: diameter of central body 31–53μ; length of processes 6–11μ; width of processes up to 13μ; number of specimens measured, 7.

Remarks. This variety forms a distinct group distinguishable from *Hystrichosphaeridium tuberiferum* only by the length of the processes. It differs from ?*Hystrichosphaeridium arundum* (Eisenack & Cookson 1960) from the Lower Cretaceous of Australia, by having much broader processes.

Hystrichosphaeridium deanei sp. nov.

Pl. 6, figs. 4, 8

Derivation of name. Named in honour of H. Deane, an early worker on fossil microplankton from the Chalk of England.

Diagnosis. Subspherical to ovoidal central body composed of thin smooth endophragm and smooth or slightly granular periphragm, the latter forming the processes. Tubular processes varying considerably in shape, sub-conical, lagenate or tubiform, open distally with entire or serrate margins. Width of processes extremely variable. Apical archaeopyle usually present.

Holotype. Geol. Surv. Colln. slide PF.3030(1). Lower Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey, at 690 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype : diameter of central body 46 by 47μ ; width of antapical process 31μ, length 35μ ; length of other processes 15–30μ. Number of processes 21. Range : diameter of central body 41–54μ, length of processes 15–45μ. Number of specimens measured, 9.

DESCRIPTION. The endophragm of the processes may be fibrous, but not strongly so. The processes vary greatly in size and shape, this variation being continuous between extremes of the range. The width of the processes on a specimen may vary from 1·5μ to 35μ ; the length of the processes is, however, more constant. The largest process is usually the antapical, it being sub-conical to lagenate in shape. In one specimen only a few of the larger processes are seen to give rise to two or three parallel branches distally. The processes reflect a tabulation of 4′, 6″, 6c, 5‴, 1p, 1⁗ and 2–4s.

H. deanei has been recorded from the Middle and Upper Cenomanian of Fetcham Mill, Surrey.

REMARKS. *H. deanei* sp. nov. resembles *H. stellatum* (Maier) recorded from the Albian and Cenomanian of Australia by Cookson & Eisenack (1962*b*). It is similar in the general form of the processes and the size of the central body, but the sub-conical to lagenate processes, common in the British forms, appear to be absent. The Australian form of *H. stellatum* does not appear to be comparable to Maier's type material from the Oligocene of Germany.

The form and the distal margins of the processes differentiate *H. deanei* from *H. tubiferum*. The reflected tabulation, however, reveals a fairly close relationship between the two species.

Hystrichosphaeridium simplicispinum sp. nov.

Pl. 9, fig. 3

DERIVATION OF NAME. Latin, *simplicis*, simple or straight and *spinous*, thorny—referring to the rather simple nature of the processes.

DIAGNOSIS. Spherical central body composed of thin smooth endophragm and periphragm, the latter forming the processes. Processes varying considerably in size and are simple, tubiform, splaying out distally and terminate with denticulate or secate margin. A number of fine sulcal processes. Apical archaeopyle usually present.

HOLOTYPE. B.M.(N.H.) slide V.51729(2). Speeton Clay, Shell West Heslerton Borehole No. 1, Yorkshire at 39 metres depth. Lower Cretaceous (Middle Barremian).

DIMENSIONS. Holotype : diameter of central body 36 by 43μ, length of processes 17–26μ. Number of processes 23, plus 4 fine sulcal processes. Range : diameter of central body 34–57μ, length of processes 8–31μ. Number of specimens measured, 4.

DESCRIPTION. The smooth periphragm of the central body and processes is sometimes slightly perforate but more commonly smooth. At the base of each process there is a characteristic thickening of the endophragm, which is here reticulate. Only four well preserved specimens have been observed, the number of wide tubular processes ranging from 22 to 24, with 1 to 6 fine sulcal processes. The antapical process is often distinctly wider than the other processes. The reflected tabulation appears to be comparable to *H. tubiferum*.

H. simplicispinum sp. nov. is present throughout the Barremian of Yorkshire.

REMARKS. In general appearance *H. simplicispinum* strongly resembles *Cordosphaeridium eoinodes* but the fibrous periphragm is absent and the number of processes is greater.

The reflected tabulation of *H. simplicispinum* is probably the same as *H. tubiferum*, but they differ in that the processes of the former are considerably more divided and not so expanded distally.

Hystrichosphaeridium patulum sp. nov.

Pl. 10, fig. 5

DERIVATION OF NAME. Latin, *patulus*, broad and spreading—with reference of the larger processes.

DIAGNOSIS. Spherical to sub-spherical central body, not exceeding 25μ in diameter, possessing a smooth thin wall and bearing two types of processes. Both types of same length and considerably expanded distally, one type much wider than the other. Distal margin entire and undulating. Length of processes one-quarter to one-half of the diameter of central body. Apical archaeopyle present.

HOLOTYPE. B.M.(N.H.) slide V.51739(1). 7 feet above base of London Clay; Whitecliff Bay, Isle of Wight.

DIMENSIONS. Holotype: diameter of central body 11·5 by 14·5μ, length of processes up to 5·5μ, number of processes 25. Range: diameter of central body 11–19μ, length of processes 4–9μ. Number of specimens measured, 8.

DESCRIPTION. This species is characterized by its broad open processes, approximately 2μ wide, and by the finer processes, up to 1μ wide. The processes are tubiform with considerably expanded distal extremities measuring up to 7μ across. The number of processes can be up to 25. The apical archaeopyle has straight edges obviously reflecting plate boundaries.

REMARKS. The small size of this species and the two types of processes are characteristic. Its processes resemble shortened and sometimes widened processes of *H. tubiferum*, and the number present is also similar. Some relationship may perhaps be inferred between these two species.

Hystrichosphaeridium arborispinum sp. nov.

Pl. 9, figs. 5, 10

DERIVATION OF NAME. Latin, *arbor*, tree ; *spinus*, spine—with reference to the tree-like appearance of the processes.

DIAGNOSIS. Sub-spherical to ovoidal central body composed of thin endophragm and granular or reticulate periphragm. Processes, composed of periphragm, hollow, tubiform, usually simple, expanding distally and terminating with complicated secate margin. Apical archaeopyle commonly present.

HOLOTYPE. B.M.(N.H.) slide V.51727(3). Speeton Clay, Shell West Heslerton Borehole No. 1, Yorkshire at 39 metres depth. Lower Cretaceous (Middle Barremian).

DIMENSIONS. Holotype : diameter of central body 39 by 39μ, length of processes 10–19μ. Range : diameter of central body 31–43μ, length of processes 10–23μ. Number of specimens measured, 4.

DESCRIPTION. The distal extremities of the processes have a distinctive ragged appearance due to the irregular shape of the secae—some being irregularly lobate, others giving off spines laterally. Specimens with fibrous processes, and more rarely with fenestrate processes, have been observed. An apical archaeopyle commonly seems to be present, but its precise nature is difficult to determine for the specimens are extremely thin walled and easily distorted. The number of processes seems to be standardized at 22 to 23, and this together with their arrangement on the surface of the central body indicate that *H. arborispinum* sp. nov. has a reflected tabulation similar to that of *H. tubiferum*.

This species has been recorded only from the Lower and Middle Barremian of Yorkshire.

REMARKS. The form of the distal extremities of the processes characterizes this species and distinguishes it from all other described species.

H. arborispinum is basically of the same type as *H. tubiferum* (Lejeune-Carpentier 1940) but has slightly broader processes which are distally much more divided.

Hystrichosphaeridium salpingophorum (Deflandre)

Pl. 10, fig. 6

1935. *Hystrichosphaera salpingophora* Deflandre : 232, pl. 9, fig. 1.
1937. *Hystrichosphaeridium salpingophorum* (Deflandre) Deflandre : 80, pl. 13, figs. 1, 3.
1940. *Hystrichosphaeridium salpingophorum* (Deflandre) ; Lejeune-Carpentier: 219, text-fig. 8.
1947. *Hystrichosphaeridium salpingophorum* (Deflandre) ; Deflandre, text-fig. 1, no. 7.
?1948. *Hystrichosphaeridium salpingophorum* (Deflandre) ; Pastiels : 37, pl. 3, figs. 3–7.
?1952. *Hystrichosphaeridium salpingophorum* (Deflandre) ; W. Wetzel : 399, text-fig. 11.
?1952. *Hystrichosphaeridium salpingophorum* (Deflandre) ; Gocht, pl. 1, fig. 19 ; pl. 2, fig. 20.
1952. *Hystrichosphaeridium salpingophorum* (Deflandre) ; Deflandre, text-fig. 11.
1955. *Hystrichosphaeridium salpingophorum* (Deflandre) ; Deflandre & Cookson : 271, pl. 2, fig. 9.
?1958. *Hystrichosphaeridium salpingophorum* (Deflandre) ; Eisenack : 401, pl. 27, figs. 5, 6.

EMENDED DIAGNOSIS. Central body spherical to ovoidal with characteristic reflected tabulation of 4′, 6″, 6c, 5‴, 1p, 1⁗ with variable number of sulcal processes. Processes well developed, tubiform, with sub-quadrate distal openings. Distal margins entire or denticulate. Number of processess present 25 to 30. Apical tetratabular archaeopyle practically always present.

HOLOTYPE. Slide AJ56, Laboratoire de Micropaléontologie, École Pratique des Hautes Études, Paris. Senonian ; France.

MATERIAL (Figured). B.M.(N.H.) slide V.51734(1). 146 feet above base of London Clay ; Whitecliff Bay, Isle of Wight.

DIMENSIONS. Range of specimens from type material (Deflandre 1937) ; diameter of central body 35 to 40μ, length of processes 25 to 30μ, the number of processes is approximately 30. Range of London Clay specimens : diameter of central body 30–44μ, length of processes 14–20μ. Number of specimens measured, 4.

DESCRIPTION. The surface of the central body may be smooth or slightly granular, and composed of two layers, the endophragm and periphragm (absent beneath the processes). The processes expand gradually towards the distal sub-quadrate opening, which is up to 18μ across in the London Clay forms. Medially the processes rarely exceed 10μ and are usually much less. The wall of the processes (composed of periphragm) is slightly fibrous. The distal margin can be serrate, undulose or even aculeate. Processes may be perforate distally.

REMARKS. The London Clay specimens have rather short and broader processes than the holotype and are perhaps a variety of *H. salpingophorum*. The ribs, illustrated by Klement (1960), extending along the length of the processes and running into the central body have not been observed. The specimen figured by Lejeune-Carpentier (1940, text-fig. 8) is very similar to the London Clay forms.

H. salpingophorum (London Clay) is generally easily distinguished from *H. tubiferum*. However certain specimens from the London Clay are transitional, often showing the circle formed at the junction of the processes and the endophragm. A close relationship with *H. tubiferum* is also indicated by the identical tabulation and intratabular processes.

The Jurassic forms formerly attributed to *H. salpingophorum* are transferred below to *Hystrichosphaeridium costatum* sp. nov.

Hystrichosphaeridium costatum sp. nov.

Pl. 10, fig. 4

?1938. *Hystrichophaeridium salpingophorum* (Deflandre) ; Deflandre : 186, pl. 10, figs. 1–3.
?1947. *Hystrichosphaeridium salpingophorum* (Deflandre) ; Deflandre, text-fig. 1, no. 6.
?1952. *Hystrichosphaeridium salpingophorum* (Deflandre) ; Deflandre, text-fig. 10.
1960. *Hystrichosphaeridium salpingophorum* (Deflandre) ; Klement : 55, pl. 7, figs. 3–5 ; text-fig. 31.
1960. *Hystrichosphaeridium salpingophorum* (Deflandre) ; Sarjeant : pl. 13, fig. 7.
1961. *Hystrichosphaeridium salpingophorum* (Deflandre) ; Sarjeant : 99, pl. 15, fig. 7.

DERIVATION OF NAME. Latin, *costa*, rib—referring to the thickenings of the periphragm.

DIAGNOSIS. Subspherical central body possessing a moderate number of fibrous tubiform processes having sub-quadrate distal openings. Distal margin denticulate with small number of recurved prolongations. Thickened ribs extending from some of the angles of the distal margins along length of processes and onto central body surface where they connect with similar ribs extending from neighbouring processes, forming mesh-like structure. Apical archaeopyle usually present.

HOLOTYPE. B.M.(N.H.) slide V.51708, from G.R. 053890, Scarborough Castle, Yorkshire. Oxford Clay (*Quenstedtoceras mariae* Zone).

DIMENSIONS. Holotype : diameter of central body 47 by 47μ, length of processes 19–28μ, number of processes 24.

DESCRIPTION. The surface (periphragm) of the central body is granular or slightly reticulate. The tubiform processes have broad bases, and splay out distally in an angular fashion, their width not exceeding 9μ medially. At the angles of the margin are commonly situated small prolongations or spines, occasionally up to 8μ long but usually considerably smaller. The processes vary considerably in width, from 1 to 9μ when measured medially. Only one or two finer processes are present on a specimen and these are probably sulcal processes. An occasional deeply furcate process has been observed in the central region of the cyst, these undoubtedly being cingulum processes. The ribs (thickenings of the periphragm) are very characteristic and form upon the surface of the central body a subpolygonal mesh-like arrangement, somewhat simulating the tabulation seen in the genus *Hystrichosphaera*, but certainly not analogous to it. An apical archaeopyle is usually present, and the reflected tabulation appears to be that typical for this genus. *Hystrichosphaeridium costatum* sp. nov. has been recorded from the Oxfordian of England, France and Germany.

REMARKS. Deflandre (1938) described *H. salpingophorum* from the Oxfordian noting the ribbed processes and an apparent similarity to the Upper Cretaceous form of this species. However, ribbing on the surface of the central body was not remarked on or shown in his illustrations (pl. 10, figs. 1–3). These forms possibly belong to *H. costatum*.

Klement (1960) described and figured specimens identical to those found in the British Oxfordian, possessing the characteristic thickenings of the periphragm.

The specimen illustrated by Lejeune-Carpentier (1940, text-fig. 7) from the Upper Cretaceous, has vague polygonal markings on the surface of the central body, but definite ribs are absent.

Sarjeant (1960, 1961) illustrated specimens of *H. costatum* as *H. salpingophorum* ; his figured specimen (1961, pl. 15, fig. 7) has been selected as holotype of the new species.

Hystrichosphaeridium readei sp. nov.

Pl. 6, fig. 3

?1940. *Hystrichosphaeridium salpingophorum* (Deflandre) ; Lejeune-Carpentier : 219, text-fig. 7.

?1940. *Hystrichosphaeridium tubiferum* (Ehrenberg) ; Lejeune-Carpentier : 218, text-fig. 5.

DERIVATION OF NAME. Named in honour of the Reverend J. B. Reade who was the first to describe and figure (1839) hystrichospheres from English flints of the Upper Cretaceous age.

DIAGNOSIS. Spherical to subspherical central body composed of smooth endophragm and periphragm. Processes, composed of the latter, slightly fibrous, cylindrical and open. Larger processes with two thickenings of periphragm extending along their length over surface of central body and joining up with similar thickenings from neighbouring processes. Processes varying in width and expanding distally, terminating in fairly complicated aculeate or secate margin. Apical archaeopyle usually present.

HOLOTYPE. Geol. Surv. Colln. slide PF.3030(2). Lower Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey, at 690 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype : diameter of central body 41 by 45μ, length of processes 23–29μ, number of processes 24. Range : diameter of central body 31–54μ, length of processes 20–35μ. Number of specimens measured, 8.

DESCRIPTION. The most characteristic feature of this species is the presence of thickenings or ribs in the periphragm. These ribs are close together near the distal end of the process and gradually diverge proximally, before separating completely on the surface of the central body, each rib passing to a different neigbouring process. Thus triangular and polygonal networks are seen on the surface of the central body. The sulcal processes are usually noticeably finer than the others and are very occasionally joined by septa, as seen in the holotype. The septa are probably modified ribs. An apical archaeopyle is usually present. The number of processes in the specimens observed varied between 23 and 27. The reflected tabulation is difficult to determine but it is probably comparable to *H. tubiferum* i.e. 4′, 6″, 6c, 5‴, 1p, 1⁗ and xs.

H. readei sp. nov. occurs in the Upper Cenomanian at Fetcham Mill, Surrey and has not been recorded lower in the succession at this locality.

REMARKS. The Cenomanian species strongly resembles and is undoubtedly related to, *H. costatum* from the Upper Jurassic. The only apparent difference between the species is in the extremities of the processes. In *H. costatum* the extremities are simply denticulate with a small number of spines, whereas in *H. readei* the extremities are considerably more complex.

H. tubiferum (Ehrenberg) as illustrated by Lejeune-Carpentier (1940, text-fig. 5), from Upper Cretaceous flint, is extremely similar to *H. readei* and could well belong to the present species.

Hystrichosphaeridium radiculatum sp. nov.

Pl. 7, fig. 8 ; Pl. 9, fig. 6

DERIVATION OF NAME. Latin, *radicula,* small root—with reference to the fibres radiating from the bases of the processes.

DIAGNOSIS. Spherical to sub-spherical central body composed of reticulate endophragm and fibrous periphragm. Processes, approximately 30 in number, composed of periphragm, fibrous, mainly hollow and open distally, simple tubiform or dividing into 2 or 3 sub-parallel branches. Processes expanding slightly distally, extremities of processes entire or denticulate.

HOLOTYPE. Geol. Surv. Coll. slide PF.3031(1). Lower Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey, at 690 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype : diameter of central body 36 by 37μ, length of processes 13–17μ. Range : diameter of central body 31–37μ, length of processes 11–17μ. Number of specimens measured, 4.

DESCRIPTION. The reticulate endophragm appears to be granular at first sight before examination in detail. Along the lengths of the processes run fibrous strands which continue on to the surface of the central body and are sometimes continuous with similar strands from neighbouring processes. The depth of the furcation of the processes varies considerably, from merely a slight distal furcation to where there appears to be two separate processes in close proximity. A rather elongate apical archaeopyle is present surrounded by 6 precingular processes. The distribution of the remainder of the processes is difficult to determine precisely.

This species is uncommon and has only been identified from the Upper Cenomanian.

REMARKS. *H. radiculatum* sp. nov. is closely related to *H. mantelli* differing in that the branched processes are more common and the fibrils of the processes continue across the surface of the central body. The reflected tabulation of the two species is probably very similar.

Hystrichosphaeridium cf. *clavigerum* (Deflandre) as illustrated by Lejeune-Carpentier (1940, text-fig. 9), resembles *H. radiculatum* in size, form of the processes, and the fibrous periphragm on the surface of the central body. However, the branching processes characteristic of *H. radiculatum*, are absent.

Hystrichosphaeridium mantelli sp. nov.

Pl. 6, fig. 6

Derivation of name. In honour of the geologist and microscopist Gideon Algernon Mantell, who did much pioneer work in interpreting the structure of Upper Cretaceous microplankton during the mid-nineteenth century.

Diagnosis. Spherical to sub-spherical central body composed of thin endophragm and granular or finely reticulate periphragm. Periphragm of processes slightly fibrous. Processes predominantly simple, tubiform, buccinate or bulbose, open distally with digitate or foliate margin. Occasionally narrow, solid, closed processes occur. Number of processes 26 or less, one process per plate area. Apical archaeopyle usually present.

Holotype. Geol. Surv. Colln. slide PF.3032(1). Lower Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey, at 840 feet depth. Upper Cretaceous (Cenomanian).

Dimensions. Holotype : diameter of central body 41 by 42μ, length of processes 13–21μ, number of processes 25. Range : diameter of central body 36–45μ, length of processes 13–26μ. Number of specimens measured, 6.

Description. At first sight the periphragm of the central body appears to be fairly heavily granular, but on closer examination the granules apparently result from a fine reticulation. The processes are erect and extremely variable in form, being tubiform, buccinate or even bulbose, usually open but occasionally closed, and simple or branched distally. The closed processes are extremely narrow, less than 1μ, and solid distally. An apical archaeopyle appears always to be present. The processes give a reflected tabulation of 6″, 6c, 5‴, 1p, 1⁗ and a variable number of sulcal processes, commonly 4–6. The detached apical region has not yet been identified.

This species has been found only in the Lower Cenomanian and is extremely uncommon.

Remarks. The reticulate nature of the central body and the fibrous processes differentiate *H. mantelli* sp. nov. from most other species. *H. radiculatum* sp. nov. is, however, fairly similar but the processes are more deeply divided, there often being 2 to 3 sub-parallel branches, and narrower.

Hystrichosphaeridium latirictum sp. nov.

Pl. 10, fig. 8

Derivation of name. Latin, *lati*, wide and *rictum*, open mouth—with reference to the considerably expanded distal margins of the processes.

Diagnosis. Central body ellipsoidal, with smooth or slightly granular wall up to one-quarter μ thick. Processes slender, tubiform, slightly fibrous, expanding considerably distally. Processes open distally and margin circular or quadrate.

HOLOTYPE. B.M.(N.H.) slide V.51740(1). Metropolitan Water Board Borehole No. 11 at 43·25 feet depth, London Clay ; Enborne, Berkshire.

DIMENSIONS. Holotype : diameter of central body 18 by 19·5μ, length of processes 9–12·5μ, breadth of processes up to 2μ, length of acuminate processes 6–8μ, number of processes 25 (and two acuminate processes). Range : diameter of central body 11–20μ, length of processes 6–13μ. Number of specimens measured, 5.

DESCRIPTION. The processes show a variation in outline and nature of distal margin which can be circularly to ovoidal, serrate, undulose or aculeate. The distal extremities of the processes are usually considerably expanded, up to 13μ wide. The length of the processes vary from one-third to two-thirds of the diameter of the central body. Besides the tubiform process there is quite often a small number of short, closed processes, as on the holotype. The latter are undoubtedly sulcal processes. An apical archaeopyle is present surrounded by 6 processes, the reflected tabulation probably being that of this genus.

H. latirictum sp. nov. has been recorded from the London Clay of Enborne and of Whitecliff Bay, Isle of Wight.

REMARKS. The size of *H. latirictum* sp. nov., in combination with the tubiform processes, is quite characteristic. *Polysphaeridium paulinae* from the Middle Jurassic of France (Valensi 1953) is similar in form but smaller with more processes, the processes being not greater than one-third of the diameter of the central body. It is possible that this species may result from misinterpretation of representatives of the genus *Stephanelytron* : the holotype, kindly lent by Prof. Deflandre for examination (in 1962), is at depth in flint and cannot be seen in full detail. Hystrichospheres with tubular processes are not otherwise known from the Middle Jurassic.

Hystrichosphaeridium recurvatum (White)

1839. *Xanthidium tubiferum* (Ehr.) : Reade, pl. 9. figs. 6, 9.
1842. *Xanthidium tubiferum palmatum* White : 39, pl. 4, div. 3, fig. 12.
1844. *Xanthidium tubiferum palmatum* White ; White, pl. 8, fig. 11.
1848. *Xanthidium palmatum* White ; Bronn : 1375.
1851. *Spiniferites palmatus* (White) Mantell : 251, text-fig. 79.
?1934. *Hystrichosphaera tubifera* (Ehr.) ; Deflandre, text-fig. 11.
1935. *Hystrichosphaera tubifera* (Ehr.) ; Deflandre : 15, pl. 7, fig. 10, ?11.
1937. *Hystrichosphaeridium tubiferum* (Ehr.) ; Deflandre : 96, pl. 13, fig. 2 ; (pl. 12, fig. 14 ; pl. 13, fig. 4).
?1940. *Hystrichosphaeridium recurvatum* (White) Lejeune-Carpentier : 221, text-fig. 6.
?1955. *Hystrichosphaeridium tubiferum* (Ehr.) ; Valensi : 592, pl. 4, fig. 2 ; pl. 5, fig. 8.
?1963. *Hystrichosphaeridium recurvatum* (White) ; Górka : 57, pl. 8, fig. 8 ; text-pl. 6, fig. 5.
1964. *Hystrichosphaeridium recurvatum* (White) ; Sarjeant : 173.

EMENDED DIAGNOSIS. Sub-spherical central body with moderate number of slender tubiform processes. Length of latter between that of radius and diameter of central body. Processes open distally, terminating with a few short orthogonal or recurved spines.

NEOTYPE. Slide AJ97, Laboratoire de Micropaléontologie, École Pratique des Hautes Études, Paris. (Figured by Deflandre 1935, pl. 7, fig. 10.) Senonian flint from the Paris Basin.

DIMENSIONS. Holotype (measured from the illustration) : diameter of central body 32 by 25μ, maximum overall diameter 75μ, length of processes 18–30μ, number of processes, 25.

DESCRIPTION. The periphragm of the central body is smooth or slightly granular and of the processes is smoother or somewhat fibrous. The processes on a specimen do not vary a great deal in their length or width, the sulcal processes not being significantly smaller. Each process has constant width along its length, widening slightly at the base but not distally, where it terminates in a rosette of short spines. An apical archaeopyle is usually present. The reflected tabulation appears to be 4′, 6″, 6c, 5‴, 1p, 1⁗ and 3–6s, and so *H. recurvatum* is provisionally placed in the genus *Hystrichosphaeridium*.

H. recurvatum has only been recorded with certainty from the Senonian of Europe.

REMARKS. Sarjeant (1964*a*), in a paper on nomenclatural problems, pointed out that on the principle of priority the correct name for this species is *H. palmatum* and not *H. recurvatum*. White (1842) referred to this species in the text as *Xanthidium recurvatum* or *palmaforme* and in the plate caption as *X. palmatum*. Thus three alternative names were suggested. Bronn (1848) was next to refer to this species. and listed it as *X. palmatum*. In 1939 a junior homonym to the latter was proposed by Deflandre & Courteville, this later being transferred to the genus *Baltisphaeridium* (Downie & Sarjeant 1963).

Lejeune-Carpentier (1940), overlooking the work of Bronn, described this species under the name of *H. recurvatum*. Subsequent workers have followed Lejeune-Carpentier and used *H. recurvatum* as the specific name instead of the correct *H. palmatum*. Downie & Sarjeant (1964) similarly use *H. recurvatum*. Since the latter is in general use and *H. palmatum* (White) Bronn has a junior homonym, it is proposed that *H. recurvatum* should be retained as the designation for this species.

A thorough search has been made to find the holotype of *H. recurvatum* from the British Senonian, figured by White (1842), but without success. It has therefore been necessary to propose a neotype for this species. The neotype proposed was first figured by Deflandre (1935, pl. 7, fig. 10) as *Hystrichosphaera tubifera* and comes from the Senonian of France (Paris Basin).

Hystrichosphaeridium sheppeyense sp. nov.

Pl. 11, fig. 3

1955. *Hystrichosphaeridium recurvatum* (White) ; Deflandre & Cookson : 269, pl. 1. fig. 11.
1961. *Hystrichosphaeridium recurvatum* (White) ; Evitt : 391, 395, pl. 4, figs. 3–5 ; pl. 5, fig. 8.

DERIVATION OF NAME. Named after the type locality, the Isle of Sheppey, Kent.

DIAGNOSIS. Ovoidal central body with smooth or slightly granular surface. Processes tubular, open distally, approximately equal in length to radius of central body, terminating in a number of orthogonal or recurved spines.

HOLOTYPE. B.M.(N.H.) slide V.51741(1). 85 feet above base of London Clay ; Sheppey, Kent.

DIMENSIONS. Holotype : overall diameter 59 by 57μ, diameter of central body 29 by 31μ, length of processes 14–18μ, width of processes up to 2μ, number of processes 26.

DESCRIPTION. The processes are relatively thick walled, the tubule being narrow and sometimes constricted. At the bases of some of the processes there are small proximal elevations or swellings. Distally the processes splay out into 2 to 7 spines or secae, up to 6μ long. An apical archaeopyle is usually present. The tabulation reflected by the processes is that of *Hystrichosphaeridium*.

REMARKS. *H. sheppeyense* sp. nov. differs from *H. recurvatum* (White) in being considerably smaller and possessing relatively short processes. The forms described and figured by Deflandre & Cookson (1955) and by Evit (1961) are identical in all respects except that the former, from the Senonian, is rather larger. Deflandre & Cookson's figured specimen has an overall diameter of 90μ, central body diameter of 44 by 51μ and processes 16–26μ in length.

Hystrichosphaeridium bowerbanki sp. nov.

Pl. 8, figs. 1, 4

DERIVATION OF NAME. After J. S. Bowerbank who was one of the first British microscopists to record hystrichospheres from the Chalk, and the first to record them from the Upper Greensand.

DIAGNOSIS. Ovoidal to elongate central body with smooth surface. Processes thin-walled, tubular, open distally, sometimes widening considerably at their base, and greater than half the central body diameter in length. They terminate in a number of orthogonal or recurved spines. Apical archaeopyle usually present.

HOLOTYPE. Geol. Surv. Colln. slide PF.3033(1). Lower Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey at 730 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype : overall diameter 85 by 78μ, diameter of central body 39 by 29μ, length of processes 24–26μ, number of processes 24. Range : overall diameter 60–85μ, diameter of central body 29–40μ, length of processes 21–26. Number of specimens measured, 5.

DESCRIPTION. The central body is characteristically ovoidal to elongate. The tubular processes are thin-walled and usually curved or bent to some extent. The distal spines are 5 to 7 in number and are up to 6μ in length. The processes are cylindrical for most of their length, 2·5 to 3μ wide and expand slightly distally to about 4μ before giving rise to spines. Proximally the processes sometimes widen

considerably and may measure up to 10μ at their contact with the central body and often show noticeable basal wrinkles. An apical archaeopyle always appears to be present. The tabulation reflected by the processes is : (4′), 6″, 6c, 5‴, 1p, 1⁗ and about 5s.

Remarks. *H. bowerbanki* sp. nov. differs from *H. recurvatum* (White) in being smaller and having wider tubular processes. It is rather similar to *H. sheppeyense* but the form of the central body is more elongate ; the processes are wider, especially at their base, and have a much thinner wall.

OTHER SPECIES

The following species are here attributed to the genus *Hystrichosphaeridium* emend. on the basis of the number of processes and general form :

Hystrichosphaeridium cf. *clavigerum* (Deflandre) ; Lejeune-Carpentier 1940. Upper Cretaceous ; Belgium.

Hystrichosphaeridium irregulare (Merrill 1895). Lower Cretaceous ; U.S.A.

Hystrichosphaeridium stellatum (Maier 1959). Oligocene ; Germany.

The following described species are doubtfully included in *Hystrichosphaeridium* emend. on the basis of the number and form of processes present :

?*Hystrichosphaeridium arundum* (Eisenack & Cookson 1960). Upper Cretaceous ; Australia.

?*Hystrichosphaeridium aquitanicum* (Deunff 1961). Lower–Upper Cretaceous ; France.

?*Hystrichosphaeridium gliwicense* (Macko 1957). Miocene ; Poland.

?*Hystrichosphaeridium hilli* (Merrill 1895). Lower Cretaceous ; U.S.A.

?*Hystrichosphaeridium polyplasium* (Maier 1959). Miocene ; Germany.

Hystrichosphaeridium claviferum (Wilkinson 1849) ; Deflandre 1946*a* (incorrectly transferred to *Baltisphaeridium* by Downie & Sarjeant 1963) and *Hystrichosphaeri-cruciatum* O. Wetzel 1933 from the description and figures both appear to be the detached apical regions of species of *Hystrichosphaeridium* emend., bearing four processes. The holotype of *H. clavigerum* is lost ; it appears likely that it represents the apical region of *H. tubiferum*, of which the species *H. clavigerum* may be regarded as a junior synonym and should therefore be rejected. *H. cruciatum*, as illustrated by Lejeune-Carpentier (1940, fig. 14), represents the apical region of an otherwise undescribed species.

Genus ***OLIGOSPHAERIDIUM*** nov.

Derivation of name. Greek, *oligo*, few or scanty ; *sphaera*, ball—with reference to the ball-like central body bearing a small number of processes.

DIAGNOSIS. Subspherical chorate cysts possessing a reflected tabulation of 4′, 6″, 5–6‴, 1p, 1⁗. Processes tubiform, open distally, intratabular, one process per plate area. Number of processes never more than 18. Archaeopyle apical.

TYPE SPECIES. *Xanthidium tubiferum complex* White 1842. Upper Cretaceous ; England.

REMARKS. Cingular processes are absent, there commonly being 6 postcingular processes. The processes are approximately of equal length on an individual but are variable within a species. They are always open and can be cylindrical to infundibular with perforate or entire walls. Endophragm confined to the central body, surrounded by periphragm which alone forms the processes. Processes never in contact with the interior of the central body.

An alternative formula for the reflected tabulation is : 4′, 6″, 5‴, 1p, 1⁗ and 0–1s. In the specimens possessing 14 processes, all are of the same size and one would expect if one sulcal process was present that this would be smaller than the other processes. This corresponds to the typical *Gonyaulax*-tabulation in which there are 6 postcingular plates, plate 1‴ sometimes being considerably reduced. The original tabulation is tentatively reconstructed in Text-fig. 1.

Oligosphaeridium complex (White)

Pl. 7, figs. 1, 2 ; Pl. 10, fig. 3 ; Text-fig. 14

1842. *Xanthidium tubiferum complex* White : 39, pl. 4, div. 3, fig. 11.
1844. *Xanthidium tubiferum complex* White ; White : pl. 8, fig. 10 ; text-figs.
1848. *Xanthidium complexum* (White) Bronn : 1375.
1940. *Hystrichosphaeridium elegentulum* Lejeune-Carpentier : 22, text-figs. 11, 12.
1946. *Hystrichosphaeridium complex* (White) Deflandre : 11.
1952. *Hystrichosphaeridium complex* (White) ; Firtion : 156, pl. 9, figs. 2, 4, 5 ; text-fig. 1A–F.
1955. *Hystrichosphaeridium complex* (White) ; Deflandre & Cookson : 270, pl. 1, figs. 9, 10.
1955. *Hystrichosphaeridium complex* (White) ; Valensi : 592, pl. 4, fig. 3.
?1958. *Hystrichosphaeridium complex* (White) ; Cookson & Eisenack : 42, pl. 12, fig. 10.
1958. *Hystrichosphaeridium complex* (White) ; Eisenack : 400 pl. 26, 400, figs. 3–5 ; pl. 25, fig. 16?
1959. *Hystrichosphaeridium complex* (White) ; Gocht : 66, pl. 3, figs. 2, 3 ; pl. 7, figs. 5, 6.
?1962. *Hystrichosphaeridium tubiferum* (Ehr.) ; Pocock : 83, pl. 15. fig. 230.
?1963. *Hystrichosphaeridium tubiferum* (Ehr.) ; Baltes, pl. 2, figs. 1–3, 5, 6.
1964. *Hystrichosphaeridium complex* (White) ; Cookson & Hughes : 46, pl. 9, fig. 6.

EMENDED DIAGNOSIS. Central body sub-spherical to ovoidal. Wall composed of thin endophragm and periphragm, the latter giving rise to processes. Processes simple or branched, cylindrical for most of their length, open and expanded distally with aculeate or secate margin. Reflected tabulation inferred 4′, 6″, 5–6‴, 1p, 1⁗. Apical archaeopyle usually present having zig-zag margin. Processes in complete specimen not exceeding 18.

NEOTYPE. Geol. Surv. Colln. slide PF.3034(1). Lower Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey, at 750 feet depth. Upper Cretaceous (Cenomanian).

Dimensions. Neotype : diameter of central body 35 by 35μ, length of processes 22–25μ. Range : diameter of central body 34–55μ, length of processes 22–43μ. Number of specimens measured, 9.

Description. In the specimens from the Cenomanian, the periphragm of the central body is smooth or very slightly granular. The processes are cylindrical for most of their length, with an expanded opening distally, the margin of which is developed into aculei and secae. The aculei and secae can be simple or branched, erect or patulate, orthogonal or even recurved. Where the processes meet the central body there is often a clearly marked ring indicating the point of divergence of the endophragm and periphragm. The wall of the processes is smooth or faintly fibrous ; their length usually measures between the radius and the diameter of the central body.

The small number of processes and the apical archaeopyle, when present, enable one readily to determine the tabulation of *O. complex* as reflected by the position of the processes.

Specimens of *O. complex* have been examined from two other horizons.

Examples from the Speeton Clay (Barremian) of Yorkshire are very similar to the forms illustrated by Eisenack (1958). The periphragm of the central body is often slightly granular and some of the processes are more deeply divided and show more variation than is usual in this species. 11 specimens were measured, the diameter of the central body being 35–62μ and the length of the processes 13–47μ.

Specimens from the London Clay (Ypresian) strongly resemble the Cenomanian forms, the processes perhaps being a little stouter. Diameter of central body 29–58μ, length of processes 23–39μ (6 specimens measured).

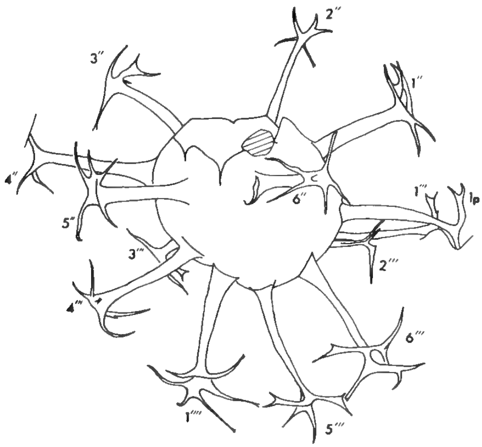


Fig. 14. *Oligosphaeridium complex* (White). A specimen from the Cenomanian, in lateral view, showing the angular apical archaeopyle and the distribution of the processes. × c. 420.

O. complex thus has a stratigraphic range from the Neocomian (Gocht 1959 and Cookson & Eisenack 1958) to the Ypresian.

REMARKS. *Oligosphaeridium complex* was first described by White (1842) as *Xanthidium tubiferum complex*. In the description of the processes White stated : " Sometimes the orifice is separated into unequal divisions of four, five and six parts, in others like one variety of *X. ramosum* before noticed ; the branching terminations are of a more complex structure, each branch having at its extremes a further ramification ; at which last I am inclined not to consider a variety of one species, but the same as the former, in an advanced state of development. " Lejeune-Carpentier (1940) briefly described forms having distal prolongations under *Hystrichosphaeridium elegantulum*. These she compared to *X. tubiferum complex* (White) and concluded that they were identical. In White's figures branching is clearly shown ; Lejeune-Carpentier's figures 11 and 12, however, suggest that some at least of the so-called distal branchings of the processes are bifurcating secae of simple processes. *H. elegantulum* was transferred to *H. complex* by Deflandre (1946) on the grounds that it was an invalid synonym, but no new diagnosis was given for *H. complex*. Firtion (1952) figured different process terminations for the species. These cannot be seen in his indistinct plates and in his description he simply states " . . . . the shell is furnished with tubiform radiating appendages ; their distal extremity very splayed-out, showing a system of fine and deep dentations."

H. tubiferum (Cookson 1953, pl. 2, fig. 24) later placed in *H. complex* (Deflandre & Cookson 1955) is of doubtful status.

Valensi (1955) figured *H. complex*, branching in at least four processes. In the same year, Deflandre & Cookson enlarged the concept of this species by including within it specimens having cathrate extremities, transitional to *H. pulcherrimum*. Their figures closely approach the London Clay forms. Cookson & Eisenack (1958) figured *H. complex* with simple processes developed distally into aculei. Eisenack (1958) Gocht (1959) and Cookson & Hughes (1964) figured specimens with simple unbranched processes, produced distally into aculei.

Neale & Sarjeant (1962) in discussing their new species *H. macrotubulum* decided that forms possessing unbranched processes did not belong to *H. complex*. Partly on this basis, partly on the granular nature of the central body, they separated *H. macrotubulum* as a distinct species. In view of the uncertainty concerning the degree of branching of the processes, both branched and simple forms have been included in *H. complex*.

Much more significant is the tabulation inferred from the positions of the processes. The specimens of *H. complex* illustrated by Firtion (1952), Deflandre & Cookson (1955), Cookson & Eisenack (1958) and Gocht (1959) are clearly forms lacking cingulum processes and possessing an apical archaeopyle.

As Deflandre & Cookson (1955) noted, transitional forms to *H. pulcherrimum* occur, which have perforate processes ; the perforations are not, however, excessively numerous and for this reason the specimens concerned were placed in *H. complex*. Comparable forms have been observed in the Cenomanian of England.

The specimens attributed to *H. complex* by Baltes (1963, pl. 3, figs. 1–3) do not belong in this species. In contrast, the forms he illustrates as *H. tubiferum* (pl. 2, figs. 1–3, 5, 6) undoubtedly belong to *Oligosphaeridium* and probably to *O. complex*.

The holotype of *O. complex* from the British Senonian illustrated by White (1842, pl. 4, div. 3, fig. 11) cannot be traced. A neotype has therefore been chosen from the Cenomanian of Surrey (England).

Oligosphaeridium reticulatum sp. nov.

Pl. 7, fig. 10

Derivation of name. Latin, *reticulatus*, net-like—with reference to the reticulate or net-like appearance of the surface of the central body.

Diagnosis. Subspherical central body composed of reticulate endophragm. Periphragm confined to processes, smooth or slightly fibrous. Processes simple, cylindrical, expanding distally and terminating in complicated aculeate or secate margin. Archaeopyle apical. Number of processes in complete specimen never exceeding 18. Inferred tabulation 4′, 6″, 5‴, 1p, 1⁗ and 0–1s.

Holotype. Geol. Surv. Colln. slide PF.3035(1). Lower Chalk, Geological Survey Borehole, Fetcham Mill, Surrey, at 840 feet depth. Upper Cretaceous (Cenomanian).

Dimensions. Holotype : diameter of central body 29 by 30μ, length of processes 15–26μ, number of processes 14. Range : diameter of central body 29–47μ, length of processes 14–26μ. Number of specimens measured, 5.

Description. The reticulate endophragm appears to be granular at low magnification, but at high magnification it is clearly seen to be finely reticulate. The cylindrical processes expand slightly proximally, forming a characteristic circle or oval on the surface of the central body. Distally they expand in the form of an open funnel often having an extremely ragged margin.

Remarks. *O. reticulatum* sp. nov. is very similar to *O. complex*, differing only in the reticulate nature of the central body and the relative shortness of the processes. It is very significant that the inferred tabulations are identical, indicating a close phylogenetic relationship.

Oligosphaeridium vasiformum (Neale & Sarjeant)

Pl. 9, fig 7 ; Pl. 10, fig. 1 ; Text-fig. 1

1962. *Hystrichosphaeridium vasiformum* Neale & Sarjeant : 452, pl. 20, fig. 1 ; text-fig. 8*b*.
1965. *Hystrichosphaeridium vasiformum* Neale & Sarjeant ; Sarjeant, text-fig. 3C.

Emended diagnosis. Sub-spherical to sub-quadrate central body composed of thin, smooth endophragm and thicker pitted periphragm. Not more than 18 processes present, composed of smooth periphragm. Processes simple, tubiform and expanding distally, distal margin bearing few spines.

HOLOTYPE. B.M.(N.H.) slide V.51709(1). Speeton Clay, Shell West Heslerton Borehole No. 1, Yorkshire, at 99·25 metres depth. Lower Cretaceous (Middle Hauterivian).

DIMENSIONS. Holotype : overall length 107·5μ, breadth 116μ, central body length 46·5μ (apical region lacking), breadth 52μ.

PARATYPE. B.M.(N.H.) slide V.51709(3) : overall length 124·5μ breadth 116μ, central body length 46·5μ (apical region lacking), breadth 46·5μ. Range ; overall lengths 107·5–130μ (7 specimens).

DESCRIPTION. The periphragm on the surface of the central body is moderately thick and pitted to a varying extent. The pits, passing through the periphragm and exposing the endophragm, vary greatly in size, being as much as 1μ across. The processes arise from root-like bases and terminate distally in 4–6 simple spines. The processes do not connect with the interior of the central body. Rarely the processes possess small, often rectangular, areas where the periphragm is extremely thin, formerly described as perforations of the processes.

An apical archaeopyle is usually present, the resulting specimens possessing 14 processes. The inferred reflected tabulation is typical of the genus.

The species has only been recorded from the Middle Hauterivian.

REMARKS. *O. vasiformum* is very similar to *O. complex* from the Barremian and is clearly related to it. The most important distinguishing features is the presence of the pitted periphragm on the surface of the central body in *O. vasiformum*. The original tabulation of this species is tentatively reconstructed in Text-fig. 1.

O. reticulatum sp. nov. is another related form, but its processes are usually noticeably shorter and stouter with a much more complex distal margin.

Oligosphaeridium macrotubulum (Neale & Sarjeant)

Pl. 9, fig. 4

1962. *Hystrichosphaeridium macrotubulum* Neale & Sarjeant : 452, pl. 20, fig. 7 ; text-fig. 8*a*.

REMARKS. A re-examination of the holotype has shown that the periphragm of the central body is pitted in exactly the same manner as in *O. vasiformum*, albeit to a lesser extent. The processes have basically the same structure as in the latter species, but are perhaps slightly stouter than is typical. The holotype does not possess an archaeopyle, there being 18 processes present, indicating the reflected tabulation typical of this genus. As only the holotype of *O. macrotubulum* was examined the range of variation cannot be ascertained, but it is probable that this species is synonymous with *O. vasiformum*.

Oligosphaeridium pulcherrimum (Deflandre & Cookson)

Pl. 10, fig. 9 ; Pl. 11, fig. 5

1955. *Hystrichosphaeridium pulcherrimum* Deflandre & Cookson : 270, pl. 1, fig. 8 text-figs, 21, 22.

1955. *Hystrichosphaeridium pulcherrimum* Deflandre & Cookson ; Valensi : 592, pl. 4, fig. 1.

MATERIAL (figured). B.M.(N.H.) slide V.51742(1). Metropolitan Water Board Borehole No. 11 at 63 feet depth, London Clay ; Enborne, Berkshire.

REMARKS. The processes of the London Clay specimens indicate a reflected tabulation of 4′, 6″, 6‴, 1p, 1⁗. The apical processes are relatively small and an apical archaeopyle is usually present. The fenestrate appearance of the processes in this species are extremely distinctive. The London Clay forms may be derived.

DIMENSIONS. London Clay forms : diameter of central body 30–48μ, length of processes 17–40μ. Number of specimens measured, 3.

Oligosphaeridium prolixispinosum sp. nov.

Pl. 8, figs. 2, 3

DERIVATION OF NAME. Latin, *prolixus*, stretched out long and *spina*, thorny—with reference to the filiform spines at the distal extremities of the processes.

DIAGNOSIS. Elongate central body bearing few open tubular processes. Processes terminating distally in a number of long thread-like spines.

HOLOTYPE. Geol. Surv. Colln. slide PF.3036(1). Lower Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey, at 840 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype: overall width 64μ, diameter of central body 40 by 20μ, length of processes 18–24μ, number of processes 17. Range : Length of central body, 33–43μ, width 20–29μ, length of processes 18–29μ. Number of specimens measured, 8.

DESCRIPTION. The periphragm of the central body and of the processes is smooth. The processes are thin-walled and have a fairly broad base up to 8μ, with characteristic basal wrinkles. There are noticeable circles beneath the processes where only endophragm is present. The processes are about 3μ in width for most of their length tapering to 2μ distally before giving rise to the filiform spines. The spines are extremely delicate, 5 to 8 in number, and up to 15μ in length. The number of processes varies from 16 to 18, the variation probably due to the number of sulcal processes present. In all specimens there is an obvious apical archaeopyle. Surrounding the archaeopyle are 6 precingular processes, then a diastema before the postcingular processes are reached. This diastema marks the position of the cingulum. The processes on the hypotract are difficult to assign to any dinoflagellate tabulation. There is no obvious antapical process, in fact 3 antapical processes usually seem to be present. The reflected tabulation appears to be (4′), 6″, 6‴, 3⁗ and 1–3s.

O. prolixispinosum sp. nov. is a rare species occurring throughout the Cenomanian of Surrey.

REMARKS. *O. prolixispinosum* sp. nov. is easily distinguishable from other species by its elongate form and small number of processes with very characteristic distal terminations. It should be noted that the basal wrinkles recorded in this species have also been seen in *Hystrichosphaeridium bowerbanki*.

At the base of the Cenomanian there have been found, together with normal examples of *O. prolixispinosum*, two specimens, which possess exactly the same elongate central body and type of processes but there are present 22 and 25 processes. This unusual number is caused by the presence of 6 cingular processes. It would thus appear that *O. prolixispinosum* is, in the Lower Cenomanian, rather an unstable species and not until later in the Cenomanian does it settle down, the cingular processes being absent.

Because of the above variation this species is rather difficult to classify since although the cingular processes are absent, it seems to be related to, or maybe even evolved from, a type possessing these processes. Two other factors are that the processes strongly resemble those found in *H. bowerbanki* and there may be 3 antapical processes present although this is uncertain. Until further information is available this species has been tentatively placed in the genus *Oligosphaeridium* because of the absence of cingular processes.

OTHER SPECIES

The following species are here attributed to the genus *Oligosphaeridium* on the basis of the number of processes and general form:

Oligosphaeridium albertense (Pocock 1962). Lower Cretaceous ; Canada.

Oligosphaeridium anthophorum (Cookson & Eisenack 1958). Upper Jurassic ; Australia and Papua.

Oligosphaeridium perforatum (Gocht 1959). Lower Cretaceous ; Germany.

Oligosphaeridium reniforme (Tasch, McClure & Oftedahl 1964). Lower Cretaceous ; U.S.A.

The following described species are doubtfully included in *Oligosphaeridium* on the basis of the number and form of the processes:

?*Oligosphaeridium asterigerum* (Gocht 1959). Lower Cretaceous ; Germany.

?*Oligosphaeridium coelenteratum* (Tasch, McClure & Oftedahl 1964). Lower Cretaceous ; U.S.A.

?*Oligosphaeridium dictyophorum* (Cookson & Eisenack 1958). Upper Jurassic ; Papua.

?*Oligosphaeridium dispare* (Tasch, McClure & Oftedahl 1964). Lower Cretaceous ; U.S.A.

?*Oligosphaeridium irregulare* (Pocock 1963 ; non Merrill 1895). Lower Cretaceous ; Canada.

?*Oligosphaeridium paradoxum* (Brosius 1963). Oligocene ; Germany.

Genus ***PERISSEIASPHAERIDIUM*** nov.

DERIVATION OF NAME. Greek, *perisseia*, abundance or surplus ; *sphaera*, ball—with reference to the rather superfluous sulcal and cingular processes.

DIAGNOSIS. Chorate cysts with sub-spherical central body composed of two membranes. Processes of two types : (i) larger, tubiform, open distally and intratabular ; one process per plate area, and (ii) smaller, closed processes restricted to sulcal and cingular regions. Tabulation reflected by tubiform processes 4′, 6″, 5‴, 1p, 1⁗. Archaeopyle apical.

TYPE SPECIES. *Perisseiasphaeridium pannosum* sp. nov.

REMARKS. This genus appears to be intermediate between *Hystrichosphaeridium* and *Oligosphaeridium*. It resembles the former in possessing both cingular and sulcal processes, but these are closed, and the latter since the tabular processes reflect a similar tabulation. It resembles *Hystrichokolpoma* in the presence of both tabular and closed processes, but the former are of a completely different type, being conical and covering most of the plate area. Also only 4 tabular postcingular processes are present in the genus *Hystrichokolpoma* whereas 5 are present in *Perisseiasphaeridium*.

Perisseiasphaeridium pannosum sp. nov.

Pl. 3, fig. 5 ; Pl. 11, fig. 8 : Text-fig. 15

DERIVATION OF NAME. Latin, *pannosus* ragged—with reference to the ragged or torn appearance of the infundibular processes.

FIG. 15. *Perisseiasphaeridium pannosum* sp. nov. A specimen from the London Clay, ventral view, showing the distribution of the processes. × c. 1000.

DIAGNOSIS. Chorate, sub-spherical to ovoidal cyst bearing two types of processes. One with broad open infundibular processes, often fenestrate distally ; the other with smaller slender processes, closed, with simple or bifurcate extremities. Apical archaeopyle present.

HOLOTYPE. B.M.(N.H.) slide V.51743(1). 155 feet above base of London Clay ; Whitecliff Bay, Isle of Wight.

DIMENSIONS. Holotype : diameter of central body 42·5 by 43μ ; length of infundibular processes 24–29μ ; length of slender processes up to 19μ. Range : diameter of central body 42–57μ ; length of infundibular processes 24–40μ ; width of infundibular processes up to 9μ proximally, 34μ distally ; length of slender processes up to 27μ ; number of specimens measured, 4.

DESCRIPTION. This species has very distinctive infundibular processes with an irregular digitate margin, each branch being further split up into evexate, bulbous or bifid secae. The secae and/or the digitae may be inter-connected, thus giving rise to a fenestrate structure. The tabulation reflected by the infundibular processes is 4′, 6″, 5‴, 1p, 1⁗. In addition there are some very slender processes, less than 1μ wide, restricted to the cingulum and sulcal zones. These processes are always closed, and are either acuminate or irregularly bifurcate. The exact number is variable and difficult to determine.

P. pannosum has only been recorded from the Ypresian of Britain.

REMARKS. This species differs from *Oligosphaeridium pulcherrimum* (Deflandre & Cookson) from the Australian Lower Cretaceous, in the nature of the fenestrate, infundibular processes. The slender cingular and sulcal processes are a characteristic feature.

OTHER SPECIES

Perisseiasphaeridium eisenacki sp. nov. The specimens described and figured by Eisenack (1958 : 402, pl. 26, figs. 1, 2) as *Hystrichosphaeridium anthophorum* Cookson & Eisenack from the Lower Cretaceous of Germany are here considered to belong to the genus *Perisseiasphaeridium* nov. and have been renamed accordingly.

Evitt (1961) pointed out that Eisenack's specimens possess definite fine cingular processes whereas the type material from the Upper Jurassic of Australia and Papua has a barren cingular zone and has been attributed to the genus *Oligosphaeridium* (see p. 77).

Genus ***LITOSPHAERIDIUM*** nov.

DERIVATION OF NAME. Greek, *litos*, plain or simple ; *sphaera*, ball—with reference to the simple arrangement of the processes on the surface of the central body.

DIAGNOSIS. Chorate cysts with spherical to sub-spherical central body composed of two membranes. Processes few in number (only one per plate area), hollow and open distally except for sulcal processes which may be closed. Reflected tabulation 3′, 6″, 5‴, 1p, 1⁗, with variable number of sulcal processes. Archaeopyle apical.

TYPE SPECIES. *Hystrichosphaeridium siphoniphorum* Cookson & Eisenack 1958. Probably Lower Cretaceous (Albian) ; Australia.

REMARKS. The presence of three apical processes and the absence of cingular processes is diagnostic of this genus, and makes it easily recognizable. The sulcal processes may be either absent or few.

Litosphaeridium siphoniphorum (Cookson & Eisenack)

Pl. 7, figs. 7, 8 ; Text-figs. 16, 17

1958. *Hystrichosphaeridium siphoniphorum* Cookson & Eisenack : 44, pl. 11, figs. 8–10.
1963. *Hystrichokolpoma* sp. B., Baltes : 587, pl. 6, figs. 6–8.
1963. *Hystrichokolpoma* sp. A., Baltes : 587, pl. 6, figs. 1–5.
1964. *Hystrichosphaeridium siphoniphorum* Cookson & Eisenack ; Cookson & Hughes : 48, pl. 9, fig. 15.

EMENDED DIAGNOSIS. Spherical to sub-spherical central body composed of thin endophragm and thick reticulate periphragm. Processes, composed of smooth periphragm, varying considerably in shape and size but commonly cylindrical or sub-conical and always hollow. Distal margin of processes entire or serrate. Hexagonal apical archaeopyle usually present. Number of processes 13, rarely 14 or 15, in specimen possessing an archaeopyle. Inferred tabulation 3′, 6″, 5‴, 1p, 1⁗ and 0–2s.

HOLOTYPE. National Museum of Victoria, Australia, specimen no. P17468, from Gingin Area, W.A., Seismic shot hole B2 at 230 ft. Horizon—probably Albian.

DIMENSIONS. Holotype : overall diameter 76μ, diameter of central body 43μ, length of processes c. 19–24μ. Paratype : overall diameter 69μ, diameter of central body 33μ, length of processes c. 14μ, operculum width 21μ.

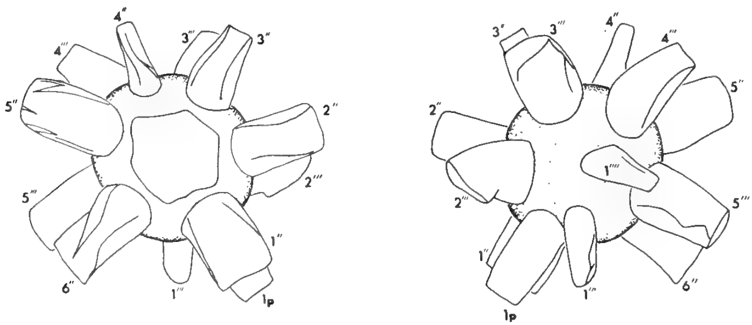


FIG. 16. *Litosphaeridium siphoniphorum* (Cookson & Eisenack). A specimen from the Cenomanian. Left, apical view, showing the six-sided archaeopyle and the arrangement of the processes ; right, antapical view. × c. 450.

Range of British Cenomanian forms : diameter of central body 21–47μ (mean 34μ), length of processes 4–25μ. Number of specimens measured, 160.

DESCRIPTION. The periphragm of the central body at first sight appears to be granular, but at high magnification is seen to be reticulate. The processes, though normally cylindrical or subconical, can be mammiform or even saucer-shaped (Text-fig. 17), the latter being 4–5μ in height. Very occasionally closed processes are present being either apical processes or small sulcal processes.

L. siphoniphorum has been recorded from the Albian of Australia and Roumania, and the Cenomanian of Australia and Britain.

REMARKS. The British Cenomanian specimens from Surrey agree fairly closely with the examples from Australia. The Surrey specimens appear to be smaller, but unfortunately the range of the Australian forms was not given in the description so no true size comparison can be made.

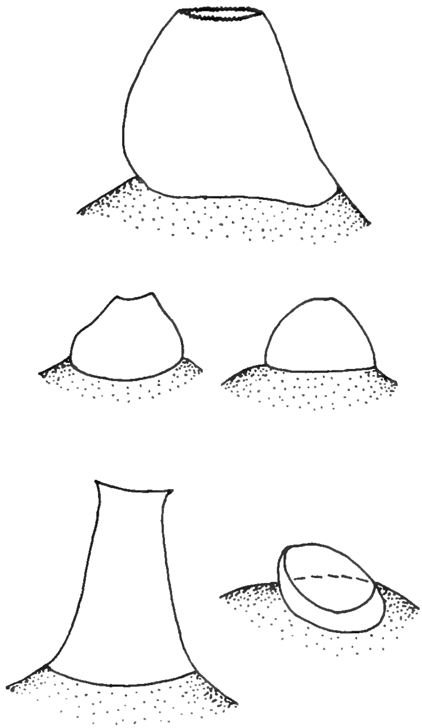


FIG. 17. *Litosphaeridium siphoniphorum* (Cookson & Eisenack). A figure illustrating the variation in the size and shape of the processes (based on specimens from the Cenomanian).

Baltes (1963) illustrated two forms (A and B) of this species from the Albian of Roumania. His species A has a central body diameter of 45–50μ and species B one of approximately 25μ. In Britain it is interesting to note that the mean of the central body diameter (34μ) falls midway between these two forms. Thus it seems likely that *L. siphoniphorum* in Britain is represented in Roumania by two geographical subspecies, corresponding to Baltes' two forms, A and B.

?*Litosphaeridium inversibuccinum* sp. nov.

Pl. 12, fig. 3

Derivation of name. Latin, *inversi*, inverted ; *buccina*, trumpet—referring to the trumpet-like shape of the processes.

Diagnosis. Sub-spherical or ovoidal central body, not exceeding 20μ in diameter, with sub-conical processes. Processes open distally, with denticulate or aculeate margin. Archaeopyle apical.

Holotype. B.M.(N.H.) slide V.51744(1). Metropolitan Water Board Borehole No. 11 at 83·25 feet depth, London Clay ; Enborne, Berkshire.

Dimensions. Holotype : diameter of central body 17 by 19μ, length of processes 7–9μ, number of processes 13. Range : diameter of central body 11–19μ, length of processes 4—9μ. Number of specimens measured, 8.

Description. The wall of the central body is usually thin, but thick walled specimens have occasionally been encountered. The processes are not in connection with the interior of the central body and seldom exceed 15. The larger processes are sub-conical and may be up to 10μ wide at the base, rapidly decreasing in width to approximately 1·5–2μ, before expanding distally into a denticulate or aculeate margin. In addition to these stout processes there are usually one or two slender ones which are possibly closed distally. The latter are probably sulcal processes. An apical tetragonal archaeopyle was seen in one specimen, the archaeopyle being surrounded by 6 precingular processes. However the remaining tabulation is obscure.

Remarks. ?*Litosphaeridium inversibuccinum* sp. nov. is easily distinguishable by its size and the form of its processes. It is tentatively placed in the genus *Litosphaeridium* because it possesses the correct number of processes to give the diagnostic tabulation of this genus, although the arrangement of the processes has, as yet, not been elucidated and a detached apical region has not been observed. The form of the processes and of the archaeopyle are both similar to those structures in *L. siphoniphorum*.

OTHER SPECIES

The following species are here tentatively referred to the genus *Litosphaeridium* on the basis of the number and type of processes :

?*Litosphaeridium crassipes* (Reade 1839). Upper Cretaceous ; England.

?*Litosphaeridium flosculus* (Deflandre 1937). Upper Cretaceous ; France.

?*Litosphaeridium truncigerum* (Deflandre 1937). Upper Cretaceous ; France.

Genus ***CORDOSPHAERIDIUM*** Eisenack 1963*b* : 261

EMENDED DIAGNOSIS. Sub-spherical chorate cysts, with central bodies composed of two distinct layers, periphragm variably developed, forming well developed processes, tubiform to buccinate, solid or hollow, intratabular and reflecting a tabulation of 1′, 6″, 6c, 6‴, (1p), 1⁗ and a variable number of sulcal processes. Apical archaeopyle haplotabular never possessing zig-zag margin.

TYPE SPECIES. *Hystrichosphaeridium inodes* Klumpp 1953. Eocene ; Germany.

REMARKS. The genus *Cordosphaeridium* differs from related genera in the form of the archaeopyle. The archaeopyle has the shape of a convex triangle with rounded corners. At first sight it appears to be precingular but by study of the process arrangement it has been shown to be apical in position. It is formed by the loss of the single apical plate, the resulting archaeopyle being termed haplotabular (latin, *haplo*, single). The processes are usually strongly fibrous and can be either open or closed distally. There is little differentiation in the size of the processes, the cingulum processes being often, but not constantly, larger. The number of processes per plate within this genus varies considerably and it is probable that at a later date it will be necessary to sub-divide this genus taking this fact into account.

This genus was proposed by Eisenack (1963*b*) for forms possessing characteristically fibrous processes. Since it has been shown that hystrichospheres are cysts of dinoflagellates, the systematics of this group should be based on the tabulation reflected by the arrangement of the processes. It is therefore considered that the reflected tabulation is a better diagnostic feature than the fibrosity of the processes and the diagnosis has been emended accordingly. Other reasons against using the fibrosity of the processes as a generic distinction are that it is very variable within this genus and also that fibrous processes have been observed in other genera which have a distinct and different tabulation.

Cordosphaeridium inodes (Klumpp)

Pl. 3, fig. 9 ; Text-fig. 18

1953. *Hystrichosphaeridium truncigerum* Cookson : 114, pl. 2, figs. 21–23.
1953. *Hystrichosphaeridium inodes* Klumpp : 391, pl. 18, figs. 1, 2.
1955. *Hystrichosphaeridium inodes* Klumpp ; Deflandre & Cookson : 277, pl. 8, fig. 7.
1961. *Hystrichosphaeridium inodes* Klumpp ; Gerlach : 186, pl. 28, figs. 4–6.
1963. *Hystrichosphaeridium inodes* Klumpp ; Brosius : 40, pl. 5, fig. 5.
1963. *Cordosphaeridium inodes* (Klumpp) Eisenack : 261, pl. 29, fig. 3.

DESCRIPTION. *C. inodes* has a fibrous body wall, bearing processes which give the reflected tabulation typical of this genus. The variability in the number of processes, noticed by Klumpp, has also been observed in the London Clay forms, especially in the sulcal region. The processes are either hollow, open distally with an ellipsoidal cross-section or taeniate. The process wálls of the London Clay specimens are extremely fibrous and appear to be thinner than in the type material, perhaps due to oxidation within the sediment.

C. inodes has been recorded from sediments ranging from the Lower Eocene to Middle Miocene in age.

MATERIAL (Figured). B.M.(N.H.) slide V.51745(1). 2 feet above base of London Clay ; Whitecliff, Isle of Wight.

DIMENSIONS. V.51745 : diameter of central body 46 by 48μ, length of processes 19–24μ. Range in type material (Klumpp 1953) : diameter of central body 52–76μ, length of processes 20–40μ. Range of London Clay forms : diameter of central body 46–76μ, length of processes 14–33μ. Number of specimens measured, 5.

Cordosphaeridium gracilis (Eisenack)

Pl. 3, fig. 8 ; Pl. 11, figs. 4, 6, 7 ; Text-fig. 19

1938. *Hystrichosphaera* cf. *ramosa* (Ehr.) ; Eisenack : 186, text-fig. 1.
1954. *Hystrichosphaeridium inodes* subsp. *gracilis* Eisenack : 66, pl. 3, fig. 17 ; pl. 10, figs. 3–8 ; 112, figs. 7, 21.
1961. *Hystrichosphaeridium inodes* subsp. *gracilis* Eisenack ; Gerlach: 187, pl. 28, fig. 6.
1963*b*. *Cordosphaeridium inodes* subsp. *gracilis* (Eisenack) Eisenack, pl. 29, fig. 2.

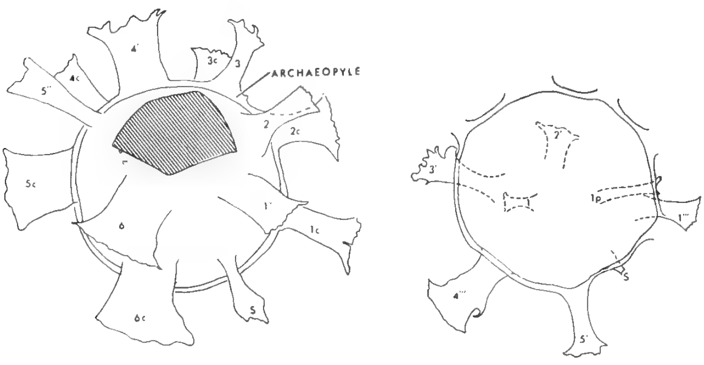


FIG. 18. *Cordosphaeridium inodes* (Klumpp). A specimen from the London Clay. Left, apical view ; right, antapical view, by transparency. × c. 650.

EMENDED DIAGNOSIS. Spherical to sub-spherical fibrous central body bearing small number of fibrous processes. Processes cylindrical, solid, erect, simple or branched and distinctly digitate ; intratabular, one per plate area, number never less than 19 or greater than 20. Archaeopyle apical, haplotabular, and reflected tabulation that of the genus *Cordosphaeridium*.

HOLOTYPE. Slide PH.10. Geologisch-Paläontologisches Institut der Universität Tübingen. Lower Oligocene ; Germany.

MATERIAL (figured). B.M.(N.H.) slide V.51746(1). 173 feet above base of London Clay ; Sheppey, Kent.

DIMENSIONS. Holotype : diameter of central body 77μ, overall diameter 166μ, length of processes 46–52μ. Range : diameter of central body 45–90μ, (mean 69μ), overall diameter 115–176μ. V.51746(1) : diameter of central body 64 by 69μ, length of processes 33–37μ. Range of London Clay specimens : diameter of central body 50–71μ, length of processes 20–43μ. Number of specimens measured, 12.

DESCRIPTION. The central body is characterized by a thick two-layered wall which is up to 2μ in thickness. The processes are strongly fibrous the fibres radiating outwards from the base of the processes over the surface of the central body, and when branched have a characteristic Y-shape. The single sulcal process is always included within the cingulum series.

REMARKS. This species was originally described and figured by Eisenack (1938*c*) as *Hystrichosphaera* cf. *ramosa*. Eisenack (1954) proposed a sub-species of *Hystrichosphaeridium inodes* to include these forms on the basis of similar wall structure. The processes were described as solid, with fibrous branched endings, and the outer layer of the wall of the central body could be thicker than the inner one. The narrow hollow space in the interior of the processes at their base and passing through to the inner wall layer that Klumpp observed in *H. inodes* was not perceived with certainty by Eisenack for *H. inodes gracilis*. Eisenack (1954) noted and figured the

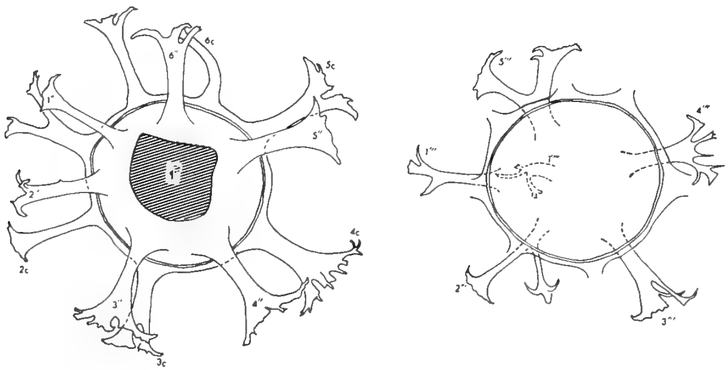


FIG. 19. *Cordosphaeridium gracilis* (Eisenack). A specimen from the London Clay. Left, apical view ; right, antapical view, by transparency. × c. 650.

archaeopyle and the operculum with a single process (plate 10, fig. 8). Gerlack (1961) similarly noticed a " pylome " in *H. inodes gracilis* (plate 28, fig. 6). In 1963, Eisenack transferred *H. inodes* and *H. inodes gracilis* to the new genus *Cordosphaeridium.*

Because of the observed differences to *C. inodes*, namely the variable thickness of the periphragm and endophragm, the absence of a narrow hollow space at the base of the processes, the solid structure and peculiar branching of the processes, it is felt that Eisenack's subspecies merits raising to the specific level.

All of Eisenack's findings are verified in the London Clay specimens. Apart from their larger size, Eisenack's and Gerlack's forms are identical with the London Clay examples.

Cordosphaeridium fibrospinosum sp. nov.

Pl. 5, fig. 5

Derivation of name. Latin, *fibra*, fibrous ; *spinosus*, thorny—with reference to the fibrous spines.

Diagnosis. Ovoidal central body with wall up to 0·5μ thick, composed of smooth endophragm and fibrous periphragm. Processes fibrous, often very broad and ovoidal in cross-section, walls perforate. Processes open distally, with entire or undulose margin. One process per plate reflecting a tabulation typical of genus. Archaeopyle apical haplotabular.

Holotype. B.M.(N.H.) slide V.51747(1). Metropolitan Water Board Borehole No. 11 at 53 feet depth, London Clay ; Enborne, Berkshire.

Dimensions. Holotype : diameter of central body 63 by 67μ, length of processes 15–28μ, width of processes 5–25μ. Range : diameter of central body 59–72μ, length of processes up to 39μ, width of processes up to 26μ. Number of specimens measured, 5.

Description. This species is characterized by fibrous, often perforate, processes which can be latispinous. The perforations show no regularity in arrangement and tend to be elongate. The cross-section of the processes is ovoidal or rarely cylindrical and then only in the narrower processes. The lengths of the processes vary considerably in different specimens but rarely exceed half the diameter of the central body. It should be noted that in the broader processes, the width often exceeds the length.

C. fibrospinosum sp. nov. has been recorded throughout the London Clay of England.

Remarks. The short, perforate processes, varying considerably in width but often very wide, make *C. fibrospinosum* an easily distinguishable species.

Cordosphaeridium cracenospinosum sp. nov.

Pl. 3, fig. 4

DERIVATION OF NAME. Latin, *cracens*, graceful or slender; *spinosus*, thorny—with reference to the appearance of the processes.

DIAGNOSIS. Sub-spherical to polygonal central body with wall composed of endophragm and periphragm, up to 1·5μ in thickness. Endophragm very thin. Archaeopyle apical haplotabular ; processes slender, buccinate, erect, or curved, solid or with fine central tubule or hollow, the last two types open distally. Distal margins foliate, bifurcate or digitate. Processes one per plate area.

HOLOTYPE. B.M.(N.H.) slide V.51748(1). Metropolitan Water Board Borehole No. 39 at 170 feet depth, London Clay ; Enborne, Berkshire.

DIMENSIONS. Holotype : diameter of central body 122 by 125μ, length of processes up to 66μ. Range : diameter of central body 75–125μ, length of processes 17–76μ. Number of specimens measured, 5.

DESCRIPTION. The large central body of *C. cracenospinosum* sp. nov. has a finely reticulate surface. In overall outline this species appears to be sub-spherical, but closer examination shows that often it tends to be polygonal. The processes are generally single, rarely branched, and in length often exceed half the diameter of the central body. The periphragm often forms a ridge on the surface of the central body where a process arises. Occasionally very fine, shorter processes are present. Many of the processes are solid, others having a narrow central cavity throughout their length or being hollow tubiform. Distally there is considerable variation, digitate endings being the commonest.

This species of *Cordosphaeridium* has been observed in samples throughout the London Clay of England.

REMARKS. *C. cracenospinosum* differs from *C. gracilis* by its thinner wall, which is only very faintly fibrous, the shape of the central body and the occasional presence of smaller, very fine, processes. It is unusual in having solid and hollow processes, the former however predominate. Process endings comparable to those in *Baltisphaeridium pectiniforme* Gerlack (1961) from the Oligocene of Germany, are occasionally encountered.

Cordosphaeridium exilimurum sp. nov.

Pl. 11, fig. 2

DERIVATION OF NAME. Latin, *exilis*, thin or meagre ; *murus* wall—with reference to the rather thin wall of the central body.

DIAGNOSIS. Ovoidal central body, composed of thin, smooth or slightly granular endophragm with fine fibrils of periphragm running over surface. Processes tubiform or buccinate, of variable width, and rarely latispinous, distally open with serrate or undulose margin. Wall of processes thin and often fenestrate.

HOLOTYPE. B.M.(N.H.) slide V.51749(1). 275 feet above the base of London Clay; Whitecliff Bay, Isle of Wight.

DIMENSIONS. Holotype: diameter of central body 44 by 54μ, length of processes 18–26μ. Range: diameter of central body 44–98μ, length of processes 16–42μ. Number of specimens measured, 7.

DESCRIPTION. Haplotabular archaeopyle and tabulation characteristic of the genus *Cordosphaeridium*. The number of processes per plate area is one, but occasionally a fine subsidiary process may be present. Fine processes also occur in the sulcal region. Both the endophragm and periphragm are extremely thin, especially the latter when forming the processes. The wall of the processes is smooth or fibrous; in the former the fibrils are only faintly developed. Whether or not the processes are always fenestrate is difficult to determine, even at high magnification, on account of the thinness of the periphragm. The processes rarely exceed half the diameter of the central body; they are up to 10μ wide meridionally and distally extremely expanded. Adjacent processes are occasionally united distally.

C. exilimurum has been recorded throughout the London Clay of England.

REMARKS. No other described species possesses fine, often perforate processes with an apical haplotabular archaeopyle and tabulation 1′, 6″, 6c, 6‴, 1⁗ and a variable number of sulcal processes. ?*C. cantharellum* (Brosius 1963) is similar in general form but possesses stronger, more cylindrical processes which are never perforate or united distally, and often have a recurved distal margin.

Cordosphaeridium latispinosum sp. nov.

Pl. 5, fig. 8

DERIVATION OF NAME. Latin, *latus*, broad; *spinosus*, thorny—with reference to the very wide processes present in this species.

DIAGNOSIS. Ellipsoidal central body having a finely striate periphragm from which arise two types of processes: broad ovoidal to quadrate ones, closed or with restricted distal opening, and slender oblate processes. Larger processes reflecting a tabulation of 1′, 6″, 6‴, 1⁗; smaller ones restricted to sulcal and cingulum regions.

HOLOTYPE. B.M.(N.H.) slide V.51746(2). 173 feet above base of London Clay; Sheppey, Kent.

DIMENSIONS. Holotype: diameter of central body 56 by 61μ, length of processes up to 22μ. Range: diameter of central body 50–77μ, length of processes 11–24μ, width of broad processes up to 27μ. Number of specimens measured, 5.

DESCRIPTION. The broad processes of *Cordosphaeridium latispinosum* sp. nov. are quadrate or ellipsoidal in cross-section proximally. They taper distally and have a slightly fibrous wall which may be perforate with small lateral spines: the broad processes are found on the apical, pre- and postcingular, posterior intercalary and antapical plate areas. The slender processes appear to be sulcal or cingular processes.

They can be simple or bifurcate, distally they are oblate or accuminate. The striae on the periphragm radiate outwards from the bases of the processes over the surface of the central body.

C. latispinosum has been recorded from the London Clay of Sheppey, Kent and Enborne, Berkshire.

REMARKS. *C. latispinosum* differs from ?*Litosphaeridium truncigerum* Deflandre 1937 from the Upper Cretaceous of France, in the nature of the broad processes. In ?*L. truncigerum* these are widely open with denticulate margins, whereas in *C. latispinosum* they are closed or have a restricted elongate opening with lateral spines developed.

Cordosphaeridium divergens (Eisenack)

Pl. 12, fig. 2

1938. *Hystrichosphaeridium* sp., Eisenack : 185, text-fig. 3.
1954. *Hystrichosphaeridium divergens* Eisenack : 67, pl. 9, figs. 13–16.
1963. *Baltisphaeridium divergens* (Eisenack) Downie & Sarjeant : 91.
1963*b* *Cordosphaeridium divergens* (Eisenack) Eisenack : 262, pl. 29, fig. 4.

DESCRIPTION. Specimens of *C. divergens* from the London Clay possess an apical haplotabular archaeopyle and the tabulation of the genus *Cordosphaeridium*. Eisenack (1954) noted and figured the archaeopyle and correctly indicated that the margin of it lay parallel to the equator. Specimens having a reticulate surface, as observed by Eisenack from the Oligocene, are also found in the London Clay. The processes are intratabular, there being at least 4 on each precingular area. In structure they compare favourably with those of the type material.

MATERIAL (Figured). B.M.(N.H.) slide V.51750(1). 157 feet above the base of London Clay ; Whitecliff, Isle of Wight.

DIMENSIONS. V.51750(1) : diameter of central body 45 by 47μ, length of processes 14–22μ. Range of London Clay forms : diameter of central body 38–52μ, length of processes 12–21μ. Number of specimens measured, 5.

REMARKS. *C. divergens* superficially resembles *Baltisphaeridium* cf. *intermedium* Deflandre (1938) from the Oxfordian, differing only in its slightly larger size. As yet species belonging to the genus *Cordosphaeridium* have not been recorded from horizons earlier than the Eocene.

Cordosphaeridium multispinosum sp. nov.

Pl. 3, fig. 6

DERIVATION OF NAME. Latin, *multi*, many or numerous ; *spinosus*, thorny—with reference to the numerous processes.

DIAGNOSIS. Sub-spherical to ovoidal central body. Thin endophragm and fibrous periphragm giving rise to numerous, more than 45, short fibrous processes.

Processes taeniate, solid, undulose with serrate or digitate distal margins, sometimes arranged in meridional rows, sometimes haphazard in position.

HOLOTYPE. B.M.(N.H.) slide V.51751(1). 173 feet above base of London Clay ; Sheppey, Kent.

DIMENSIONS. Holotype : diameter of central body 56 by 59μ, length of processes up to 15μ. Range : diameter of central body 45–59μ, length of processes up to 24μ. Number of specimens measured, 4.

DESCRIPTION. The processes are numerous, generally simple with parallel edges expanding proximally and distally. Some of the processes are regularly linked proximally in such a manner as to give rise to six long rows, running from apex to antapex. Between these rows the arrangement of the other processes appears to be haphazard. There appear to be 2, rarely 3, processes per plate area. The maximum width of the processes is 7μ, and their length one-quarter to one-third (rarely up to one-half) the diameter of the central body. Occasionally fine, acuminate processes are present on the central body. There is a well developed archaeopyle with an uninterrupted margin.

C. multispinosum sp. nov. has been recorded from the London Clay of Whitecliff Bay, Isle of Wight, Hampshire and the Isle of Sheppey, Kent.

REMARKS. In the linear arrangement of some of the processes and the haphazardous nature of others *C. multispinosum* differs from all other species of *Cordosphaeridium*.

?***Cordosphaeridium fasciatum*** sp. nov.

Pl. 7, figs. 5, 6

DERIVATION OF NAME. Latin, *fasciatus*, striped—with reference to the striped appearance of the central body due to the thickenings of the periphragm.

DIAGNOSIS. Spherical to sub-spherical central body composed of reticulate endophragm of fibrous periphragm. Processes, composed of periphagrm, smooth or slightly fibrous, short, wide and tubiform, always hollow and denticulate distally.

HOLOTYPE. B.M.(N.H.) slide V.51719(1). Speeton Clay, Shell West Heslerton Borehole No. 1, Yorkshire, at 42·5 metres depth. Lower Cretaceous (Lower Barremian).

DIMENSIONS. Holotype : diameter of central body 40 by 40μ, length of processes 11–16μ, number of processes 19. Range : diameter of central body 35–47μ, length of processes 12–25μ. Number of specimens measured, 6.

DESCRIPTION. From the base of each process, thickenings of the periphragm radiate over the surface of the central body joining together with similar thickenings from neighbouring processes. The reticulate nature of the endophragm can sometimes be observed where the periphragm thins midway between processes and also at the bases of the processes when one is able to view directly down the centre of a vertical process (Pl. 7, fig. 6). The processes have parallel or sub-parallel sides

throughout their length. There are 18 to 20 processes, an apical archaeopyle usually being present. The shape and form of the archaeopyle is difficult to determine and a detached apical region has not, as yet, been observed. However the archaeopyle is thought to be haplotabular and the spines to have an inferred reflected tabulation of 1′, 6″, 6c, 5‴, 1⁗ and 0–2s.

?*C. fasciatum* sp. nov. has only been recorded from the Lower Barremian of Yorkshire.

REMARKS. The short, wide tabular processes differentiate this species from ?*C. eoinodes* (Eisenack) and the nature of the periphragm on the central body is probably different although this was not commented on in the original diagnosis or description. The nature of the periphragm on the surface of the central body and when composing the processes of *Hystrichosphaeridium radiculum* sp. nov. and *H. mantelli* sp. nov. is very similar to *C. fasciatum* perhaps indicating a relationship between the three species. Each form possesses a distinctive type of process and the two forms of *Hystrichosphaeridium* have a greater number of processes than does *C. fasciatum*. The type of archaeopyle is a very important factor in determining the above relationships but unfortunately the exact type of archaeopyle has not been determined as yet.

?*C. fasciatum* is thought to belong to *Cordosphaeridium* on account of the probable presence of a haplotabular archaeopyle, the number of processes and the fibrous nature of the periphragm so commonly observed in species of this genus.

OTHER SPECIES

The following species are here tentatively referred to the genus *Cordosphaeridium* Eisenack 1963, emend. on the basis of the number and type of processes:

?*Cordosphaeridium cantharellum* (Brosius 1963). Oligocene ; Germany.
?*Cordosphaeridium difficile* (Manum & Cookson 1964). Upper Cretaceous ; Arctic Canada.
?*Cordosphaeridium diktyoplokus* (Klumpp 1953). Eocene ; Germany.
?*Cordosphaeridium diktyoplokus* subsp. *latum* (Klumpp 1953). Eocene; Germany.
?*Cordosphaeridium eoinodes* (Eisenack 1958). Lower Cretaceous ; Germany.
?*Cordosphaeridium erectum* (Manum & Cookson 1964). Upper Cretaceous ; Canada.
?*Cordosphaeridium floripes* (Deflandre & Cookson 1955). Miocene ; Australia.
?*Cordosphaeridium floripes* subsp. *breviradiatum* (Cookson & Eisenack 1961). Eocene ; Australia.
?*Cordosphaeridium microtriaina* (Klumpp 1953). Eocene ; Germany.

Genus ***POLYSPHAERIDIUM*** nov.

DERIVATION OF NAME. Greek, *polys*, many ; *sphaero*, ball—with reference to the central spherical body which bears numerous processes.

DIAGNOSIS. Chorate cysts possessing sub-spherical to ovoidal central body and bearing numerous processes all similar in size. Number of processes per plate area

greater than one, not normally more than four. Processes hollow, open or closed distally, process cavity not connecting with interior of central body. Archaeopyle, when present, apical with angular margin.

TYPE SPECIES. *Polysphaeridium subtilum* sp. nov. Eocene (Ypresian) ; England.

REMARKS. The processes are typically fairly short and expand distally, terminating by a serrate or spinous margin. The number of processes present makes it extremely difficult for the reflected tabulation to be determined, but is undoubtedly basically the same as that possessed by *Hystrichosphaeridium tubiferum* (Ehr).

As this genus now stands it contains a large number of species having in common an archaeopyle and a large number of hollow processes, but otherwise unrelated. At some future date, fuller knowledge of this genus will undoubtedly necessitate its subdivision, perhaps on the basis of process form.

Polysphaeridium subtile sp. nov.

Pl. 11, fig. 1

DERIVATION OF NAME. Latin, *subtilus*, thin or slender—with reference to the slenderness of the processes.

DIAGNOSIS. Central body, sub-spherical to sub-rectangular, with wall composed of extremely thin smooth endophragm and thin granular periphragm. Processes not in connection with interior, slender, open distally, with serrate margin. Average length of processes, one-fifth to one-third the diameter of central body. Number of processes greater than 60.

HOLOTYPE. B.M.(N.H.) slide V.51752(1). 178 feet above base of London Clay; Sheppey, Kent.

DIMENSIONS. Holotype : diameter of central body 47–48μ, length of processes 10–16μ. Range : diameter of central body 31·5–50μ, length of processes 6–16μ. Number of specimens measured, 5.

DESCRIPTION. Simple, slender, tubiform processes possessing a usually serrate distal margin. The latter is occasionally entire, and may be circular or oval. The width of the processes never exceeds 2μ. The processes do not appear to be arranged in any regular pattern.

REMARKS. *P. subtile* sp. nov. is distinguished from all other species by the number and form of the open processes present.

Polysphaeridium pastielsi sp. nov.

Pl. 4, fig. 10

1948. *Hystrichosphaeridium pseudhystrichodinium* (Deflandre) ; Pastiels : 43, 3, figs. 12–15.

DERIVATION OF NAME. In honour of André Pastiels, who made pioneer studies in the Eocene microplankton of Belgium.

DIAGNOSIS. Ovoidal central body with smooth or granular surface. Apical archaeopyle with zig-zag margin. Processes numerous, all of one type ; simple open, tapering distally to narrow neck before spreading slightly to an opening with entire or serrate margin. Processes sometimes united proximally, slightly fibrous.

HOLOTYPE. B.M.(N.H.) slide V.51753(1). 99 feet above base of London Clay ; Sheppey, Kent.

DIMENSIONS. Holotype : diameter of central body 37–43μ, length of processes 10–14μ. Range : diameter of central body 31–43μ, length of processes up to 19μ. Number of specimens measured, 5.

DESCRIPTION. The processes broaden proximally, often quite considerably, and may measure up to 9μ in width but the latter is very variable. An apical archaeopyle is present.

REMARKS. The Ypresian forms illustrated by Pastiels (1948) as *Hystrichosphaeridium pseudohystrichodinium* strongly resemble the London Clay forms. The holotype of Deflandre has long supple processes, thinning regularly towards the extremity which is simple, or fluted, or with a very small fork. *P. pastielsi* is therefore a separate species which superficially resembles *H. pseudohystrichodinium*.

?*P. asperum* (Maier) is described as having an oval granular central body. The processes are open, tapering, terminating distally in 2–3 spines. This distal margin is not unlike the denticulate lip sometimes observed in *P. pastielsi*. The two species may even be conspecific.

P. simplex (White) as illustrated by Gerlach (1961) and by Brosius (1963) are both probably conspecific with *P. pastielsi*. They differ from White's holotype which possesses longer and fewer processes with greatly expanded distal openings.

Polysphaeridium pumilum sp. nov.

Pl. 7, figs. 3, 4

?1955. *Hystrichosphaeridium recurvatum* (White) ; Deflandre & Cookson : 269, pl. 1. fig. 12.

DERIVATION OF NAME. Latin, *pumilus*, dwarfish or little—with reference to the small size of this species.

DIAGNOSIS. Subspherical central body having numerous small open tubular processes. Processes terminating distally in a slightly recurved more or less entire margin. Length of processes less than half that of the maximum body diameter.

HOLOTYPE. Geol. Surv. Colln. slide PF.3037(1). Lower Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey at 750 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype : overall diameter 40 by 34μ, diameter of central body 25 by 19μ, length of processes 8–10μ. Number of processes c.44. Range : overall diameter 30–40μ, diameter of central body 17–25μ, length of processes 7–10μ,

width of processes 1–1·5μ, number of processes 38–44. Number of specimens measured, 3.

DESCRIPTION. The central body has a smooth surface. The processes are tubular with a thin wall. They widen slightly both proximally, at the junction with the central body, and distally up to about 2μ. The distal termination of a process superficially strongly resembles that of *Hystrichosphaeridium sheppeyi* sp. nov., but on closer examination the presence of spines has not been observed. The distal margin is probably entire or slightly denticulate. The number of processes present indicate that each precingular and postcingular plate area bears two processes. An archaeopyle has not been observed with certainty.

REMARKS. This species is clearly differentiated from all other species by its size and the number and type of processes present. It appears to be very similar to Deflandre & Cookson's second series of specimens described as *Hystrichosphaeridium recurvatum* (White) ; however the Australian examples of Lower Cretaceous age seem to be larger, although the correct number of processes for the species is present. Deflandre & Cookson (1955, pl. 1, fig. 12) illustrate a specimen with seemingly similar processes to the British Cenomanian examples.

Polysphaeridium laminaspinosum sp. nov.

Pl. 8, fig. 8

DERIVATION OF NAME. Latin, *lamina*, blade ; *spinosus*, thorny—referring to the flattened blade-like appearance of the processes.

DIAGNOSIS. Spherical to sub-spherical central body composed of reticulate endophragm. Processes numerous, approximately 36 in number, composed of periphragm ; cylindrical, smooth and delicate, terminating in entire margin. Characteristic circular impression occurring where process arises from central body.

HOLOTYPE. Geol. Surv. Colln. slide PF.3052. Lower Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey, at 650 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype : diameter of central body 27 by 27μ, length of processes 11–15μ, number of processes 36. Range ; diameter of central body 23–28μ, length of processes 11–17μ. Number of specimens measured, 6.

DESCRIPTION. The endophragm appears to be granular until examined under high magnification when the reticulate nature becomes apparent. The processes are broadly tubular, up to 5μ in width, usually flattened and are often bent. A few of the processes are clearly truncated at their distal extremity, but most splay out slightly and have a corrugated entire margin. A 6-sided apical archaeopyle has been observed in one specimen. The number of processes present indicate that there are two per plate.

P. laminaspinosum is a rare species found throughout the Cenomanian of Fetcham Mill, Surrey.

REMARKS. The size, number and nature of the processes make it easy to distinguish *P. laminaspinosum* from all previously described species. The processes are longer and more distinctly tubular than is usual for this genus. If more species of this form are discovered a new genus should be erected to differentiate these types from the typical species of *Polysphaeridium*.

OTHER SPECIES

The following species are here tentatively referred to the genus *Polysphaeridium* on the basis of the form of the processes although an apical archaeopyle has not been recorded in any of them.

?*Polysphaeridium asperum* (Maier 1959). Miocene ; Germany.
?*Polysphaeridium deflandrei* (Valensi 1947). Middle Jurassic ; France.
?*Polysphaeridium* cf. *elegantulum* (Wiler 1956). Tertiary ; Germany.
?*Polysphaeridium fabium* (Tasch, McClure & Oftedahl 1964). Lower Cretaceous ; U.S.A.
?*Polysphaeridium fluctuans* (Pastiels 1948). Eocene ; France.
?*Polysphaeridium follium* (Tasch, McClure & Oftedahl 1964). Lower Cretaceous ; U.S.A.
?*Polysphaeridium fucosum* (Valensi 1955). Cretaceous ; France.
?*Polysphaeridium marsupium* (Tasch, McClure & Oftedahl 1964). Lower Cretaceous ; U.S.A.
?*Polysphaeridium major* (Lejeune-Carpentier 1940). Upper Cretaceous ; Belgium.
?*Polysphaeridium paulinae* (Valensi 1953). Middle Jurassic ; France.
?*Polysphaeridium perovatum* (Tasch, McClure & Oftedahl 1964). Lower Cretaceous ; U.S.A.
?*Polysphaeridium polypes* (=*H. recurvatum* subsp. *polypes* Cookson & Eisenack 1962). Lower–?Upper Cretaceous ; Australia.
?*Polysphaeridium rhabdophorum* (Valensi 1955). Cretaceous ; France.
?*Polysphaeridium simplex* (White 1842). Upper Cretaceous ; England.
?*Polysphaeridium tribrachiosum* (Tasch, McClure & Oftedahl 1964). Lower Cretaceous ; U.S.A.
?*Polysphaeridium zoharyi* (Rossignol 1962). Pleistocene ; Israel.

Genus ***DIPHYES*** Cookson 1965 : 85

EMENDED DIAGNOSIS. Chorate cysts with ovoidal to spherical central body composed of two layers. Processes numerous, 1 to 4 per plate area, hollow and either open or closed distally. Large antapical process occurring opposite apical archaeopyle.

TYPE SPECIES. *Hystrichosphaeridium colligerum* Deflandre & Cookson 1955. Eocene ; Australia.

REMARKS. The genus *Diphyes* is here restricted to include forms possessing two types of processes—numerous fine ones and a single large antapical. *D. nudum* Cookson does not possess any processes at all and certainly does not belong in this genus.

Diphyes colligerum (Deflandre & Cookson)

Pl. 4, figs. 2, 3

1953. *Hystrichosphaeridium* sp. C. Cookson : 115, pl. 2, figs. 29, 30.
1955. *Hystrichosphaeridium colligerum* Deflandre & Cookson : 278, pl. 7, fig. 3.
1962. *Hystrichosphaeridium colligerum* Deflandre & Cookson ; Cookson & Eisenack : 44, pl. 2, fig. 9.
1963. *Baltisphaeridium colligerum* (Deflandre & Cookson) Downie & Sarjeant : 91.
1965. *Diphyes colligerum* (Deflandre & Cookson) Cookson : 86, pl. 9, figs. 1–12.

EMENDED DIAGNOSIS. Ovoidal to spherical central body with wall composed of thin endophragm and outer finely reticulate periphragm. Processes composed of periphragm, numerous, simple, hollow, open or closed distally. One single broad antapical process. Total number of processes exceeding 50.

HOLOTYPE. P.16301, National Museum of Victoria, Australia. Princetown Member of Dilwyn Clay, Lower Eocene ; Point Ronald, Vic. Dept. of Mines bore, Victoria.

MATERIAL (Figured). B.M.(N.H.) slide V.51754(1). 157 feet above base of London Clay ; Whitecliff Bay, Isle of Wight.

DIMENSIONS. Holotype : diameter of central body 33μ, overall diameter 56μ, length of antapical process 20μ, width of antapical process 13μ, length of small processes approx. 13μ. Range : diameter of central body 30–33μ, overall diameter 56–59μ, length of small processes approx. 13μ. Figured specimens diameter of central body 33 by 37·5μ, length of antapical process 16μ, width of antapical process 15μ, length of small processes 11–15μ. Range of English specimens : diameter of central body 29–41μ, length of antapical process 16–21μ, width of antapical process 8–15μ, length of small processes 8–15μ.

DESCRIPTION. An apical archaeopyle and the large antapical process enable easy orientation of specimens of this species. The antapical process is hollow, cylindro-conical, occasionally closed, and bears small tubules, 2–3μ long, towards the distal extremity. The tubules can take the form of simple conical protuberances or can have slightly bifurcate extremities. The smaller processes are commonly simple, occasionally united proximally, and may be open or closed distally. They are slender but do vary in width, and in specimens possessing open processes they taper to a distal neck before terminating with a sightly expanded opening. The distal margin may be finely serrate or entire. Both types of processes are slightly fibrous and do not communicate with the interior of the central body. There are commonly 4, regularly distributed, processes for each precingular plate area ; 2–4 for the postcingular plate areas and a constant 2 in the cingular plate areas.

REMARKS. The diagnosis of *Diphyes* has been emended to relate the process arrangement to a dinoflagellate tabulation, and to draw attention to the single antapical process.

In the original diagnosis, the smaller processes are said to be closed. The figure by Deflandre & Cookson (1955, pl. 7, fig. 3) seems to indicate, however, that the processes are open, as in the examples from the London Clay. Cookson & Eisenack (1961, pl. 2, fig. 9) figured *H. colligerum* with the processes definitely open. The species may well be confined to examples with open processes after re-examination of the holotype. Cookson (1965, pl. 9, figs. 1–3) illustrates forms with distinctively larger antapical processes not unlike those of *Litosphaeridium siphoniphorum* (Cookson & Eisenack). Because of the larger size of this process she has incorrectly considered it to represent a second portion of the central body and has erected a new genus diagnosed as possessing bipartite cysts. The forms from the London Clay, the holotype of *D. colligerum* and the specimen illustrated by Cookson & Eisenack (1961, pl. 2, fig. 9) are probably more typical of the species and show without doubt that the " posterior portion of the shell " is in fact an enlarged antapical process. This species has been recorded from the Upper Cretaceous (probably Senonian) and Eocene of Australia, and in England only from the Eocene.

This species is easily distinguishable from all other types of dinoflagellate cysts.

OTHER SPECIES

The following species is here tentatively referred to the genus *Diphyes* on the basis of the numerous processes and single distinctive antapical process :

?*Diphyes monstruosum* (Tasch, McClure & Oftedahl 1964). Lower Cretaceous ; U.S.A.

Genus ***DUOSPHAERIDIUM*** nov.

DERIVATION OF NAME. Latin, *duo*, two ; *sphaera*, ball—with reference to the biospheroidal form of the test.

DIAGNOSIS. Proximate cyst composed of two more or less spheroidal parts, neither bearing processes. Anterior part with apical archaeopyle. Posterior part similar in shape with small circular antapical opening present.

TYPE SPECIES. *Diphyes nudum* Cookson 1965. Upper Eocene ; Australia.

REMARKS. The type species was formerly placed in the genus *Diphyes* by Cookson (1965) because of the apparent resemblance of its posterior part to the antapical process of *Diphyes colligerum*. However, the latter is a chorate cyst whereas the former is proximate, a difference considered by the authors to be of profound significance in the development history of dinoflagellate cysts and thus to preclude classification in the same genus.

Genus ***TANYOSPHAERIDIUM*** nov.

DERIVATION OF NAME. Greek, *tanyo*, long or stretched out ; *sphaera*, ball—with reference to the elongate nature of the central body exhibited by this genus.

DIAGNOSIS. Chorate cysts with elongate central body composed of endophragm and periphragm, the latter also forming the processes. Processes cylindrical, open distally and arranged in more or less regular circular manner around central body. Number of processes variable, usually one or two (occasionally three) per plate area. Archaeopyle apical.

TYPE SPECIES. *Tanyosphaeridium variecalamum* sp. nov. Upper Cretaceous (Cenomanian) ; England.

REMARKS. The marked feature of this genus is the elongate nature of the central body. Although the processes are arranged in a distinct circular manner on the surface of the central body, the tabulation is difficult to determine. The number of antapical processes, however, appears to be 3 or 6. Usually there is one or two processes per plate area, but occasionally three may be present. Neither a detached apical region nor a complete specimen has, so far, been observed.

Tanyosphaeridium variecalamum sp. nov.

Pl. 6, fig. 7 ; Text-fig. 20

DERIVATION OF NAME. Latin, *varius*, different ; *calamus*, reed—with reference to the rather variable extremities of the processes.

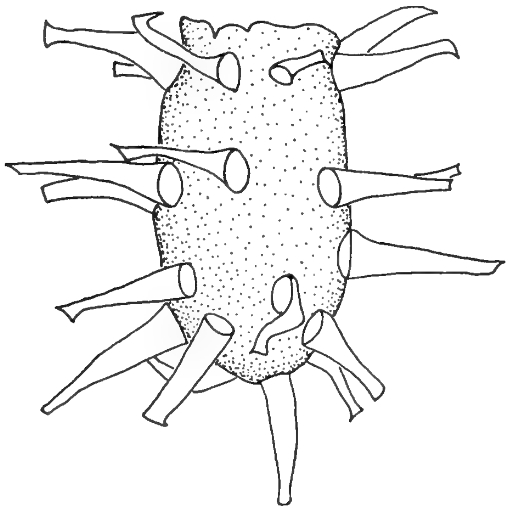


FIG. 20. *Tanyosphaeridium variecalamum* sp. nov. Holotype, lateral view, showing the circular arrangement of processes around the central body. × c. 1450.

DIAGNOSIS. Elongate central body with granular surface. Processes, moderate in number, cylindrical, expanding slightly distally and terminating with serrate, aculeate or truncated margin.

HOLOTYPE. Geol. Surv. Colln. slide PF.3035(2). Lower Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey, at 840 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype : length of central body 34μ, breadth 14μ, length of processes 12–16μ, number of processes 26. Range : length of central body 30–43μ, breadth 14–20μ, length of processes 12–24μ. Number of specimens measured, 13.

DESCRIPTION. The central body is composed of thin endophragm surrounded by granular periphragm. The processes are composed of smooth periphragm, and have an oval cross-section, there being characteristic oval areas on the surface of the central body beneath the processes, marking the initial divergence of the periphragm from the endophragm. The processes have fairly broad bases and taper distally before expanding slightly before terminating. Distally the processes may be truncated, terminate with one or two spines or splay out, the margin being serrate. The number of processes normally varies between 20 and 31, but one specimen has been observed with as many as 38.

An apical archaeopyle is always present, surrounded by 6 precingular processes. Medially there is a definite ring of 6 cingular processes and therefore 9–14 processes on the hypotract. The arrangement of the hypotractal processes is difficult to interpret ; however there appears to be either 3 or 6 antapical processes. The number of sulcal processes appears to be 5–7. This species is therefore variable in the number of processes it possesses and is able to have either one or two processes per plate in certain areas.

This species is present throughout the Cenomanian of England.

REMARKS. The only similar species is *T. isocalamus* (Deflandre & Cookson) from the Lower Cretaceous of Australia. The figures of the Australian form (Deflandre & Cookson 1955, pl. 2, figs. 7, 8) show that more processes are present than in *T. variecalamum* and that the extremities of the processes are more uniformly truncated.

Tanyosphaeridium regulare sp. nov.

Pl. 3, fig. 3

DERIVATION OF NAME. Latin, *regularis*, according to rule—with reference to the regular arrangement of the processes.

DIAGNOSIS. Elongate central body with granular surface, bearing numerous tubular, usually curved processes. Processes terminating with somewhat serrate margin.

HOLOTYPE. B.M.(N.H.) slide V.51755(1). 270 feet above base of London Clay ; Whitecliff Bay, Isle of Wight.

DIMENSIONS. Holotype : length of central body 36·5μ, breadth of central body 23·5μ, length of processes 14–19μ, number of processes approximately 65. Range : length of central body 30–44μ, breadth of central body 21–24μ, length of processes 12–19μ. Number of specimens measured, 4.

DESCRIPTION. The periphragm of the central body is granular and bears a number of quite large tubercles. The periphragm of the processes is smooth. The processes have relatively broad bases, up to 4μ wide and taper distally being 1–1·5μ wide for most of their length. At their distal extremities they widen slightly and have a somewhat serrate margin. The processes are arranged in circular series around the central body, indicating a reflected dinoflagellate tabulation. Two or, more rarely, three processes are present for each plate area.

T. regulare has been recorded from the London Clay of Whitecliff Bay and of Enborne, Berkshire.

REMARKS. The distinctive elongate nature of the central body of *T. regulare* is typical of this genus. *T. regulare* differs from *T. variecalamum* in having more processes, and from *T. isocalamus* comb. nov. in having slenderer processes with more complex terminations.

OTHER SPECIES

The following species are here attributed to the genus *Tanyosphaeridium* on the basis of the shape of the central body and the form of the processes :

Tanyosphaeridium ellipticum (Cookson 1965). Upper Eocene ; Australia.

Tanyosphaeridium isocalamus (Deflandre & Cookson 1955). Lower Cretaceous ; Australia.

Genus ***HOMOTRYBLIUM*** nov.

DERIVATION OF NAME. Greek, *homos*, same or similar ; *tryblion*, cup or bowl—with reference to the formation of two, almost equal, hemispheres after rupture of the cyst.

DIAGNOSIS. Sub-spherical chorate cyst with central body composed of thin endophragm and surrounding periphragm which gives rise to processes. Processes intratabular, cylindrical to tubiform, open distally, reflecting a tabulation of 3′, 6″, 6c, 6‴, 1p, 1⁗ and 1 to 5s. Processes not in communication with cavity of the central body. Archaeopyle epitractal, suture running just above cingulum processes.

TYPE SPECIES. *Homotryblium tenuispinum* sp. nov. Eocene ; England.

DESCRIPTION. The genus *Homotryblium* is unusual in possessing an epitractal archaeopyle which has a compound operculum composed of the apical and precingular plate series. It is an easily recognizable genus because of the nature of this archaeopyle and the possession of only 3 apical processes. Dinoflagellate cysts possessing epitractal archaeopyles are rare. *Rhaetogonaulax* gen. nov. and *Dichadogonyaulax* gen. nov. are both described by Sarjeant, in a later section, as possessing epitractal archaeopyles ;

Homotryblium tenuispinosum sp. nov.

Pl. 4, fig. 11 ; Pl. 12, figs. 1, 5, 7 ; Text-fig. 21

DERIVATION OF NAME. Latin, *tenuis*, thin; *spinosus*, thorny—with reference to the rather slender processes.

DIAGNOSIS. Spherical central body with wall composed of thin layers—smooth inner endophragm, outer strongly granular periphragm. Processes erect or curved, tubiform, simple, open distally with serrate or aculeate margin, rarely perforate Width of processes variable.

HOLOTYPE. B.M.(N.H.) slide V.51756(1). Metropolitan Water Board Borehole No. 11 at 53 feet depth, London Clay ; Enborne, Berkshire.

DIMENSIONS. Holotype : diameter of central body 41 by 48μ, length of processes 20–25μ. Range : diameter of central body 41–57μ, length of processes 13–32μ. Number of specimens measured, 8.

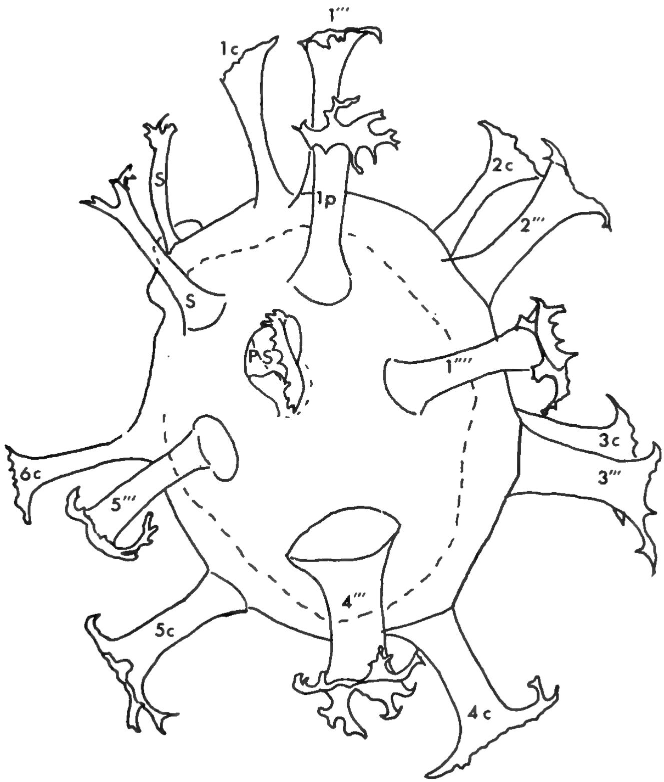


FIG. 21. *Homotryblium tenuispinosum* sp. nov. A specimen from the London Clay, antapical view. × c. 950.

DESCRIPTION. The processes are restricted to one per plate area and indicate a reflected tabulation of 3′, 6″, 6c, 5‴, 1p, 1⁗ and 1–5s. The equatorial and sulcal processes are frequently more slender than the others. Distally the processes often have a margin bearing short bifid aculei. The length of the processes is about half the diameter of the central body. The margin of the archaeopyle is interrupted on the epitract by a short projection, the sulcal tongue (Evitt). This has a corresponding sulcal notch on the hypotract. The number of sulcal processes varies from 1 to 5. In some specimens the plates readily separate, save for the three apicals which have never been observed as individual plates.

H. tenuispinosum sp. nov. has only been recorded from the London Clay of England.

REMARKS. From the nature of the archaeopyle, the coarsely granular wall and the tabulation, *H. tenuispinosum* is distinct from all previously described species.

Homotryblium pallidum sp. nov.

Pl. 12, figs. 4, 6 ; Text-fig. 22

DERIVATION OF NAME. Latin, *pallidus*, pale—with reference to the rather light colour of the central body after staining.

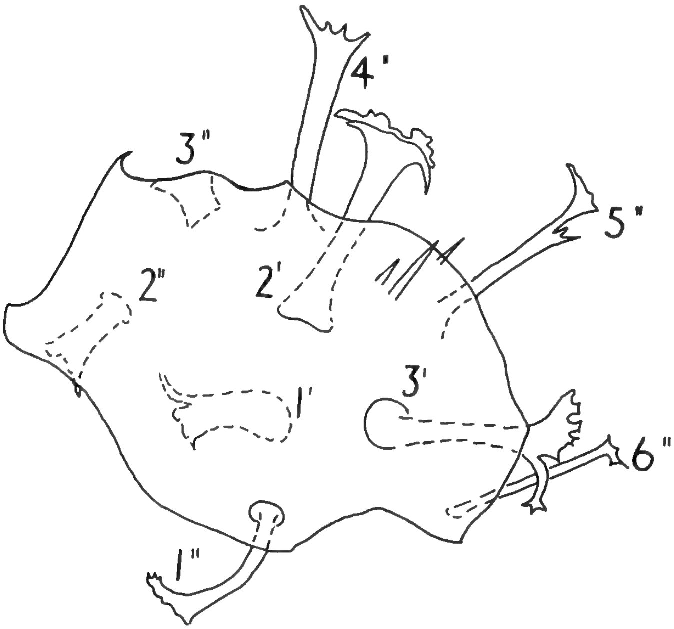


FIG. 22. *Homotryblium pallidum* sp. nov. A specimen from the London Clay. Internal view of the epitractal operculum ; slender acuminate ancillary processes are present. × c. 950.

DIAGNOSIS. Sub-spherical to ovoidal central body composed of thin inner endophragm and granular periphragm. Processes of variable width, simple, tubiform, forming a circle where they arise from central body. Archaeopyle epitractal and processes reflecting generic tabulation.

HOLOTYPE. B.M.(N.H.) slide V.51756(1). Metropolitan Water Board Borehole No. 11, at 53 feet depth, London Clay ; Enborne, Berkshire.

DIMENSIONS. Holotype : diameter of central body 45 by 48μ, length of processes up to 25μ. Range : diameter of central body 40–49μ, length of processes 16–34μ. Number of processes 5. Number of specimens measured, 5.

DESCRIPTION. *H pallidum* sp. nov. exhibits similar tabulation to *H. tenuispinosum* of 3′, 6″, 6c, 5‴, 1p, 1⁗ with almost invariably only three sulcal plates. The central body, which takes stain only slightly having a very thin wall, has granules up to 0·5μ in height and 0·5μ to 1·5μ apart. The processes are cylindrical tubiform and in length closely approach the radius of the central body. Distally they are variable, in some specimens having an entire irregular margin, in others a serrate, aculeate or digitate margin. Besides the tubiform processes there are often present 1 to 5 slender small acuminate processes. The latter can occur on the hypo- or epitract.

This species has only been recorded from the London Clay of England.

REMARKS. *H. pallidum* differs from *H. tenuispinosum* in having a thinner wall, generally broader processes with more variable distal margins, and a well marked proximal circle where they arise from the central body. It also differs by having some very slender acuminate processes. The specimens with processes having entire circular or serrate margins appear to be closely related to *Hystrichosphaeridium choanophorum* Deflandre & Cookson (1954) from the Miocene of Australia, although Gerlack (1961) recognized what appears to be an apical archaeopyle in this species.

Genus *CALLAIOSPHAERIDIUM* nov.

DERIVATION OF NAME. Greek, *kallaion*, cockscomb ; *sphaera*, ball—with reference to the crests or ribs on the surface of the central body.

DIAGNOSIS. Chorate cysts with sub-spherical central body composed of two layers. Processes intratabular and of two types : (i) cingular processes large and tubular, open distally, and (ii) apical, precingular, postcingular and sulcal processes solid. Antapical processes absent. Reflected tabulation inferred from arrangement of processes is 1′ (—2′), 6″, 6c, 5‴, 1p, 0⁗ and 0–1s. Thickenings of periphragm join all except cingular processes. Archaeopyle epitractal, suture just above cingular processes.

TYPE SPECIES. *Hystrichosphaeridium asymmetricum* Deflandre & Courteville 1939. Upper Cretaceous ; France.

REMARKS. The form of the processes, the epitractal archaeopyle and the absence of antapical processes make this a very distinctive genus. The thickenings of the periphragm joining the processes are also a noteworthy feature, though not peculiar to this genus.

Callaiosphaeridium asymmetricum (Deflandre & Courteville)

Pl. 8, figs. 9, 10 ; Pl. 9, fig. 2

1939. *Hystrichosphaeridium asymmetricum* Deflandre & Courteville : 100, pl. 4, figs. 1, 2.

DESCRIPTION. This species, previously recorded only from the Senonian flints of France, has now been observed in the Speeton Clay of Yorkshire (Hauterivian and Lower and Middle Barremian) and in the Cenomanian of Surrey. All specimens agree fairly well with the original description given by Deflandre & Courteville (1939).

In the Barremian forms the large tubular processes tend to be considerably less spinous than the Upper Cretaceous forms and more globular, especially along the ribs. The term globular refers to small spherical spaces between the endophragm and the periphragm. In the Cenomanian examples, the distal spines may measure up to 20μ. A noticeable feature in many of the British examples, not commented on in the original description, is the elevation of the ribs joining the hypotractal processes to form quite well developed septa.

An archaeopyle is usually present, formed by the loss of the portion of epitract just above the tubular cingular processes. The five postcingular processes are joined by ribs forming a pentagon from which radiate ribs to the cingular processes. Along one of these ribs are usually situated two processes—one posterior intercalary and one sulcal. The apical region possesses a hexagon of 6 precingular processes and an apical process which is sometimes deeply divided and arises from the centre of the hexagon. The reflected tabulation therefore is : 1′ (—2′), ? 6″, 6c, 5‴, 1p, 0⁗ and 0–1s.

DIMENSIONS. Holotype : diameter of central body about 40μ, length of tabular processes 22–34μ. Range of Speeton Clay forms : diameter of central body 34–43μ, length of cingular processes 11–20μ. Number of specimens measured, 4. Range of Cenomanian forms : diameter of central body 37–58μ, length of cingular processes 10–32μ. Number of specimens measured, 5.

OTHER SPECIES HITHERTO PLACED IN *HYSTRICHOSPHAERIDIUM*

The following species formerly attributed to *Hystrichosphaeridium* Deflandre 1937 are here removed from this genus and referred to the following genera :

Achomosphaera alcicornu (Eisenack 1954). Oligocene ; E. Prussia, USSR.

Achomosphaera grallaeforme (Brosius 1963). Oligocene ; Germany.

?*Achomosphaera hirundo* (Eisenack 1958). Lower Cretaceous ; Germany.
Hystrichosphaera leptoderma (Maier 1959). Oligocene ; Germany.

?*Hystrichokolpoma xiphea* (Maier 1959). Oligocene ; Germany.
Cymatiosphaera membranacea (Philippot 1949). Oligocene ; Germany.

CONCLUSIONS

The characteristics and known stratigraphical distribution of the 10 genera here considered are summarized in the accompanying Table. At present, the stratigraphic distribution of the genera cannot be correlated coherently with the variation in structure. As more species are attributed to these genera and the stratigraphic range of each genus becomes better known perhaps evolutionary relationships will become more obvious.

At present no species belonging to these genera have been found earlier than the Middle Jurassic. Three genera are present in the Upper Jurassic ; *Polysphaeridium*, perhaps a primitive form, bearing numerous processes, and *Hystrichosphaeridium* and *Oligosphaeridium* both reflecting similar tabulations and possessing 4 apical processes. From the latter two genera perhaps are derived the remaining genera with the exception of *Diphyes*. After the Jurassic, although the tabulation remained basically the same, the number of apical plates appears to have become more variable and is probably an important systematic character. The genera *Diphyes*, *Cordosphaeridium* and *Homotryblium* have not been recorded, with certainty, from the Mesozoic.

Dinoflagellate cysts belonging to the genera discussed are relatively abundant from the Upper Jurassic to the end of the Eocene, but appear to become less common thereafter. After more detailed morphological studies have been performed their importance to world-wide stratigraphy should be considerable.

TABLE 3

Genera	Tabulation	Form Archeopyle	Form of processes	Shape of central body	Stratigraphic Range
Polysphaeridium	Numerous processes	Apical	Hollow, open or closed	Sub-spherical	Upper Cretaceous–Eocene (Cenomanian–Ypresian) Middle Jurassic–?Pleistocene
Hystrichosphaeridium	4′ (–5′), 6″, 6c, 5–6‴, 1p, 1⁗ and xs.	Apical	Tubular	Sub-spherical	Upper Jurassic–Oligocene (Upper Jurassic–?Pliocene)
Oligosphaeridium	4′, 6″, 5–6‴, 1p, 1⁗	Apical	Tubular	Sub-spherical	Upper Jurassic–Ypresian
Callaiosphaeridium	1′ (–2′), 6″, 6c, 5‴, 1p, 0⁗ and 0–1 s	Epitractal	Cingular processes tabular, remainder are solid	Sub-spherical	Upper Jurassic–Upper Cretaceous Barremian–Senonian
Litosphaeridium	3′, 6″, 5‴, 1p, 1⁗ and xs	Apical	Tubular	Sub-spherical	Lower Cretaceous–Upper Cretaceous Albian–Cenomanian (Albian–?Ypresian)
Tanyosphaeridium	Numerous processes 3⁗ or 6⁗	Apical	Tubular	Elongate	Lower Cretaceous–Eocene Ypresian
Perisseiasphaeridium	4′, 6″, xc, 5‴, 1p, 1⁗ and xs	Apical	Tubular with closed cingular and sulcal processes	Sub-spherical	Lower Cretaceous–Eocene–Ypresian
Diphyes	Numerous processes 1⁗	Apical	Hollow, open or closed. Large antapical processes	Sub-spherical	Eocene Ypresian (?Lower Cretaceous–Ypresian)
Cordosphaeridium	1′, 6″, 6c, 6‴, (1p), 1⁗ and xs	Apical	Tubular and solid	Sub-spherical	Eocene Ypresian–Oligocene (?Lower Cretaceous—?Miocene)
Homotryblium	3′, 6″, 6c, 6⁗, 1p, 1⁗ and 1–5 s	Epitractal	Tubular	Sub-spherical	Eocene?Ypresian

The character and known distribution of "hystrichospheres" with tubular processes. The stratigraphic range first shown is the confirmed one, and that shown in parenthesis is tentative.

VI. DINOFLAGELLATE CYSTS WITH *GONYAULAX*—TYPE TABULATION

By W. A. S. SARJEANT

INTRODUCTION

The dinoflagellate genus *Gonyaulax* was originally proposed by Diesing (1866) in the following terms :

> " Animalcula solitaria libra symmetrica. Corpus immutabile, ovatum, ecaudatum, ciliatum, lorica, tabulata, sulco, hiante transversali in pagina dorsali obliquo in pagina ventrali bis geniculato et altero longitudinali, ab anfracto anteriori sulci transversalis ad extremitiatum anticam excurrenti, tripartita inclusum cilii e sulcis prominentibus. Os terminale. Flagellum unum pone os. Anus . . . . Ocellus nullus. Partitio ignota. Mariolae."

The type species selected was *G. spinifera* (Claperide). An amended and much fuller diagnosis was subsequently proposed by Kofoid (1911) :

> " Body variously shaped, spheroidal, polyhedral, broadly fusiform, elongated with stout apical and antapical prolongations, or dorsoventrally flattened. Apex rounded or truncate symmetrically or asymmetrically, never acutely symmetrically pointed. Antapex rounded, flattened, or pointed symmetrically or asymmetrically. Girdle usually equatorial, descending, displaced distally one to seven times its own width, and sometimes with slight overhang. Transverse furrow impressed or not ; longitudinal furrow usually slightly indenting the epitheca, often flaring distally, well developed, reaching to or approaching the anatpex. Thecal wall consisting of one to six apical plates (1′–6′), none to three anterior intercalaries (1a–3a), six precingulars (1″–6″), six girdle plates (1g–6g), six postcingulars (1‴–6‴), one posterior intercalary (1p) and one antapical (1⁗). The longitudinal furrow occupies the whole of the ventral area, which slightly indents the epitheca and consists of one anterior, about four intermediate, and one posterior plate. The midventral plate (1′) of the apical series is usually a narrow plate extending posteriorly to a junction with the anterior plate of the ventral area, thus parting precingulars 1″ and 6″. When guarded by lateral ridges it simulates an anterior extension of the longitudinal furrow. It bears at its apex a delicate extension, the closing platelet which cover the apical region.
>
> Surface smooth or rugose with major thickenings along suture lines and minor ones on plates forming a regular or irregular polygonal mesh of varying size, often with vermiculate longitudinal elements predominating, sometimes spinulate. Furrows with or without lists which in many species are ribbed or spinulate. One or more antapical spines sometimes present, rarely with sheathed spines of the *Ceratocorys* type. Plates porulate, with pores in centres, angles or nodes of the mesh. A peculiar large ventral pore occurs to the right of the midventral line, usually near the suture between apical 1′ and the plate to its right. Theca divided obliquely in fission. Ecdysis frequently seen. Chromatophores yellow to dark brown, often dense. In fresh, brackish and marine waters from boreal to tropical regions."

Fossil forms, from the Upper Jurassic (Oxfordian) of France, were first attributed to this genus by Deflandre (1938). A tabulation pattern corresponding exactly to that of *Gonyaulax* was found to be exhibited by four species, which were named *G. jurassica*, *G. cladophora*, *G. eisenacki*, and *G. pachyderma*. A feature noted was the frequent absence of precingular plate 3″, but the significance of this was not immediately recognized. A subsequent study by Deflandre of French Kimmeridgian sediments yielded further new species with the characteristic tabulation : and subsequent studies by various authors showed that fossils with a tabulation of this type were present from the Upper Triassic to the Oligocene, attaining greatest abundance in the Upper Jurassic and Lower Cretaceous.

A number of other genera with a corresponding or closely similar tabulation have since been proposed. The genus *Ctenidodinium* was proposed by Deflandre (1938) for Upper Jurassic forms having a strong, denticulate crest on the posterior margin of the cingulum, but with only a low ridge on its anterior margin. These forms split by schism along the line of the cingulum. Klement (1960) demonstrated that the tabulation of these forms corresponded to that of *Gonyaulax* and proposed abandonment of the name *Ctenidodinium*.

The genus *Lithodinia* was formulated even earlier (Eisenack 1935) for forms with a partially silicified shell from the Middle Jurassic (Dogger) of the Baltic. Subsequently Eisenack (1961) stated that he considered *Lithodinia* to be congeneric with *Gonyaulax*. The author was courteously allowed to examine the genotype of *Lithodinia* during a visit to Tübingen in 1962 ; the tabulation certainly corresponds closely to the *Gonyaulax* pattern.

The genus *Microdinium* was proposed by Cookson & Eisenack (1960) for forms having a tabulation pattern as follows ; 1′, 6″, ?6c, 6‴, 1p, 1⁗, the shell opening by loss of the apical plate. This tabulation accords with that specified by Kofoid (1911) and the genus is thus technically invalid ; however, the majority of fossil species attributed to *Gonyaulax* have three to four apical plates.

The genus *Hystrichosphaera*, which has a *Gonyaulax*-type tabulation, is treated with in an earlier section. There are in addition six other described fossil genera showing a tabulation resembling, but not exactly corresponding to, that of *Gonyaulax* :

Cryptarchaeodinium Deflandre 1939, described from the French Upper Jurassic (Kimmeridgian), has the tabulation 4′, 6″, 7‴, 1–?2p, ?1⁗. This differs from that of *Gonyaulax* in the presence of an extra postcingular plate and in the presence of three plates (not yet clearly designated) in the antapical region.

Eisenackia Deflandre & Cookson 1955, described from the Lower Tertairy of Australia, has the tabulation ?3′, 6″, ? 6 c, 6‴, 1–2p, 1⁗. It differs from *Gonyaulax*, and corresponds to *Cryptarchaeodinium*, in having three plates in the antapical region, but differs from the latter genus in the possession of only two or three apical plates.

Leptodinium Klement 1960, described from the Upper Jurassic of Australia, has the tabulation 4′, 6″, ?6c, 5‴, 1p, 1⁗. It differs from *Gonyaulax* in the lack of any anterior intercalary plate and the presence of one fewer postcingular plate.

Pluriarvalium Sarjeant 1962, from the Upper Jurassic of England, has the tabulation 5′, 1–3a, 6″, 6c, 6‴, 1p, 1p.v., 1—?6p.c., 1⁗. It is characterized by possession of a posterior circle of small plates surrounding the antapex.

Glyphanodinium Drugg 1964, from the Paleocene of California, has the tabulation ?1′, 5″, 6c, 6‴, 1p, 1p.v., 1⁗. It is distinguished by the possession of only five precingular plates and the lack of an anterior intercalary plate.

There are in addition a number of genera whose tabulation is incompletely known but which appear comparable to the *Gonyaulax* type. *Eodinia* Eisenack 1936, from the Middle Jurassic of Germany, has a thick, porate wall and shows little sign of tabulation ; there is no true cingulum, a helicoid suture being present instead. Comparison to the *Gonyaulax*-type cysts is afforded by the overall shape and the presence of an apical horn.

Rhynchodiniopsis Deflandre 1935, from the Upper Cretaceous of France, has raised, denticulate crests with spines arising at points of crest junction around the transverse furrow. The surface is reticulate : the tabulation undetermined. In shape and presence of an apical horn, it compares with the fossil cysts of *Gonyaulax* type : there are no apparent distinguishing characters.

Raphidodinium Deflandre 1936, from the Upper Cretaceous of France, has about a dozen spines arising at crest nodes, these spines being of sufficient length to render this a chorate cyst. Sutures are, however, present : the tabulation has not been determined.

Hystrichodinium Deflandre 1935, again from the Upper Cretaceous of France, is another spinose form, the spines arising from sutures in considerably greater numbers. The tabulation appears comparable to that of *Gonyaulax* but has hitherto remained undetermined.

Belodinium Cookson & Eisenack 1960, from the Upper Jurassic of Australia, has a circular cingulum, plates differentiated by raised crests, an apical horn and a " flattened, membranous expansion " on the hypotract. This genus appears inadequately characterized. This comment applies equally to *Carpodinium* Cookson & Eisenack 1962*b*, from the Lower Cretaceous of Australia whose tabulation is incompletely known and whose other characters in no wise differ from those specified for *Gonyaulax*.

Heliodinium Alberti 1961, from the Lower Cretaceous of Germany, resembles *Hystrichodinium* but has flattened, dagger-like processes arising from the crests. The tabulation is again undetermined but appears closely similar to that of *Gonyaulax*.

There are thus a considerable number of genera of fossil dinoflagellates which possess or approach the *Gonyaulax* tabulation pattern. Those forms directly allocated to the genus *Gonyaulax* were originally considered to be the fossil remains of the motile stage of that genera. It was nonetheless recognized that the shell wall characteristically contained an opening of some kind, formed by median fission or by loss of a plate or a group of plates. Following the demonstration by Evitt (1961) that the occurrence of such openings (archaeopyles) indicated cysts, it became clear

that the fossil *Gonyaulax* species were in fact cysts. Subsequently Evitt & Davidson (1964) demonstrated from studies of modern dinoflagellates that the genus *Gonyaulax* formed cysts of more than one type, but certainly including chorate cysts attributable to the genus *Hystrichosphaera* ; and Sarjeant (1965, text-fig. 3) showed that the arrangement of processes in the chorate Lower Cretaceous species *Oligosphaeridium* (formerly *Hystrichosphaeridium*) *vasiforum* indicated a *Gonyaulax*-type motile stage.

A somewhat confusing nomenclatural situation thus presents itself. On the one hand, it is now clear that a single modern dinoflagellate genus, with a constant tabulation, may form cysts which are of such distinctly different morphology as to merit classification into different form-genera ; it is arguable, on this basis, that the cyst characters indicate different evolutionary lineages and fully justify splitting of the modern genus. On the other hand, should the modern genus be retained unamended, it might well be considered that retention of separate generic names for the fossil cysts, which are simply stages in the life cycle, is unjustifiable.

The terms of the " International Code of Botanical Nomenclature " recognize the existence of genera of three types—natural " Linnaean " genera ; organ genera, representing either parts of plants or stages in their life cycles ; and form genera, defined on morphology alone. Certain genera of dinoflagellate cysts may prove, as in the case of *Hystrichosphaera*, to have a determinable relationship to a living genus defined on its motile stage. However, it remains to be proved that a particular cyst type can be produced *only* by one particular motile type ; it is entirely possible that the same cyst type might be produced by related, but different, motile types. The dinoflagellate cysts, whether recent or fossil, are best treated as form genera and species, unless or until special provisions are framed for their treatment.

These problems have been discussed at length by Deflandre (1964), Evitt & Davidson (1964) and Norris (1965). A first step towards their solution was taken by Deflandre (1964 : 5) :

> " . . . je place dans le genre *Gonyaulacysta* nov. gen. (générotype : *Gonyaulax jurassica* Defl. 1938) toutes les espèces fossiles à tabulation de *Gonyaulax* répresentées par des thèques à côtes saillantes plus ou moins ornementées (pectinées, épineuses, denticulées etc . . .) munie d'un archéopyle (3ième plaque pré-équatorial)."

This proposal provides a partial answer to the problem ; however, the fossil species previously classed into *Gonyaulax* include not only forms with a precingular archaeopyle formed by loss of plate 3″, but also forms with apical, epitractal and cingular archeopyles. Moreover, the diagnosis remains too wide in terms of tabulation and overall morphology ; forms like *Hystrichodinium* and *Heliodinium* would become homonyms, should their tabulation be shown to correspond to that of *Gonyaulax*. A more restricted diagnosis of *Gonyaulacysta* is therefore proposed in the section that follows ; the status of the genera mentioned earlier is reviewed ; and new genera are set up to accommodate species which do not accord with the revised concept of *Gonyaulacysta*, either in tabulation, ornamentation or mode of archaeopyle formation.

A. Genera with precingular archaeopyle

Genus *GONYAULACYSTA* Deflandre 1964 : 5

Emended diagnosis. Proximate dinoflagellate cysts, spherical, ovoidal, ellipsoidal or polyhedral, with the tabulation 3–4′, 0–1a, 6″, 6c, 6‴, 1p, 0–1 p.v., 1⁗. Cingulum strongly or weakly helicoid. Cingular plates (6c) well or poorly marked ; ventral surface may show division into additional small plates. Sulcus generally but not constantly extending onto epitract. Apical horn frequently, but not constantly present ; median and antapical horns lacking. Sutures in form of low ridges ; bearing crests of varied form (smooth denticulate or spinous ; perforate or imperforate) ; or marked by lines of spines of varied form. Height of spines or crests always less than $\frac{1}{4}$ of shell width. A precingular archaeopyle formed by loss of plate 3″. (Archaeopyle not always present.) Surface smooth, granular, nodose, punctate or reticulate.

Type species. *Gonyaulax jurassica* Deflandre 1938. Upper Jurassic (Oxfordian) ; France.

Remarks. The generic diagnosis is emended to include reference to tabulation and to exclude forms characterized by very high crests, very long sutural spines, or a general spine cover. Forms with high crests are referred to *Heslertonia* gen. nov. ; forms with long sutural spines to *Heliodinium*, *Hystrichodinium* or *Raphidodinium* : and forms with a general spine cover to *Acanthogonyaulax*. Forms according to this diagnosis but with an apical archaeopyle are referred to *Meiourogonyaulax* ; forms with an epitractal archaeopyle to *Rhaetogonyaulax* and *Dichadogonyaulax* ; and forms with a cingular archaeopyle to *Ctenidodinium*.

Gonyaulacysta gongylos sp. nov.

Pl. 13 figs. 1, 2 ; Text-fig. 23.

1961. *Gonyaulax* sp., Sarjeant : 97, pl. 13, fig. 15 ; text-fig. 6.

Derivation of name. Greek, *gongylos*, ball, in reference to the spherical shape.

Diagnosis. A *Gonyaulacysta* having an almost spherical theca, with short blunt apical horn. Tabulation 4′, 1a, 6″, 7c, 6‴, 1p, 1⁗ ; plate boundaries usually bearing low, denticulate crests, Plate 1′ elongate and corresponding to anterior prolongation of sulcus ; plate 4′ very small, occupying horn tip. Plate 1‴ reduced and elongate ; its boundary with sulcus not marked by a crest. Sulcus and cingulum both relatively broad ; cingular plate 7c small and pentagonal in shape.

Holotype. B.M.(N.H.) slide V.51708(2). Lowest Oxford Clay ; Castle Cliff, Scarborough, Yorks. Upper Jurassic (Lower Oxfordian).

Dimensions. Holotype : overall length 47μ, length of horn 5μ ; overall breadth 45μ ; breadth of cingulum c. 5μ. The few other specimens seen proved too severely damaged for measurement, but appear of comparable dimensions.

DESCRIPTIONS. Theca almost spherical, but having a somewhat polygonal appearance because of the angularly set crests. The horn is tipped by plate 4′; extensions of plates 1–3′ form its base. The anterior intercalary plate, 1a, is quadrate and separated from the horn by plate 3′. Of the six precingular plates, plate 6″ is reduced, plate 3″ notably large and forming the anterior dorsal surface. It is arguable whether there are five or six postcingular plates, since plate 1‴ is defined only by the angles formed by plates 2‴ and 1p with the furrow and sulcus. Plate 3‴ is large and forms the posterior dorsal surface: plate 2″ is reduced to accommodate the quadrate posterior intercalary plate. The antapex is occupied by a single polygonal plate.

The cingulum is broad and laevorotatory, its two ends differing in antero-posterior position by the cingulum's width. A pentagonal plate is present between the sulcus and the more posterior end of the cingulum; this is here designated plate 7c, but since its form does not correspond with that of the other cingular plates, a special name might be merited. The sulcus is narrow in its anterior portion, broadening to contact with the cingulum and thenceforward remaining of constant breadth in its posterior portion.

The surface of the periphragm is generally smooth, but bears a sparse scatter of coarse granules. The crests are strong but low, with well marked denticulations, resembling in form crest type f. of *Gonyaulacysta jurassica* (cf. Sarjeant, 1961, text-fig. 1).

REMARKS. *Gonyaulacysta gongylos* sp. nov. is an unusually small species characterized by its overall shape, its apical tabulation, and the presence of plate 7g. Reexamination of the holotype under a more powerful microscope has led to a fuller elucidation of the structure, in particular with regard to the crest form and the pattern of postcingular plates (a presumed plate boundary being shown to be merely a fold).

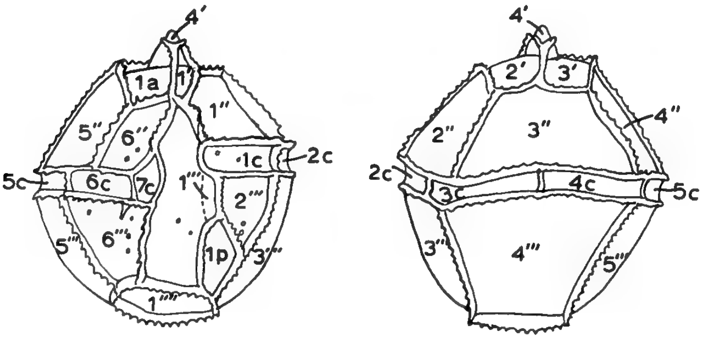


FIG. 23. *Gonyaulacysta gongylos* sp. nov. Tabulation. Left, ventral view; right, dorsal view. × c. 800.

This species remains infrequent, only a very few severely damaged specimens having been encountered subsequently. For this reason also, the character of the archaeopyle remains to be confirmed ; allocation to *Gonyaulacysta* is made on the basis of tabulation and general morphology. It shows a similarity to a group of Upper Jurassic–Lower Cretaceous species *Gonyaulacysta jurassica*, *G. eisenacki*, *G. cretacea* and *G. helicoidea*) in crest form and in the reduction of plate 1″, but differs from them in shape and presence of plate 7c.

Gonyaulacysta palla sp. nov.

Pl. 13, figs. 3, 4 ; Text-fig. 24

DERIVATION OF NAME. Greek, *palla*, ball, in reference to the overall shape.

DIAGNOSIS. A *Gonyaulacysta* with almost spherical theca and prominent apical horn. Tabulation 4′, 1a, 6″, ?6c, ?7‴, 1p, 1⁗ ; plate boundaries demarcated by crests formed of very short spines arising from low ridges. Plate 1′ elongate, occupying anterior prolongation of sulcus and relatively large ; plate 4′ small, occupying horn tip. Sulcus and cingulum of moderate breadth. Plate 1‴ small and quadrate : posterior intercalary plate correspondingly small. Plate 2‴ somewhat larger than plate 1‴, but remaining markedly smaller than other postcingular plates. Number of postcingular plates probably seven, but presence of crest between plates 4‴ and 5‴ not confirmed.

HOLOTYPE. B.M.(N.H.) slide V.51718(2). Speeton Clay, Shell West Heslerton Borehole No. 1, West Heslerton, Yorks., at 42·50 metres depth. Lower Cretaceous (Lower Barremian).

DIMENSIONS. Holotype : overall length 62μ, length of horn, 10μ ; overall breadth 50μ ; breadth of cingulum c.4μ. Range of dimensions observed ; overall lengths 60–64μ, overall breadths 46–52μ.

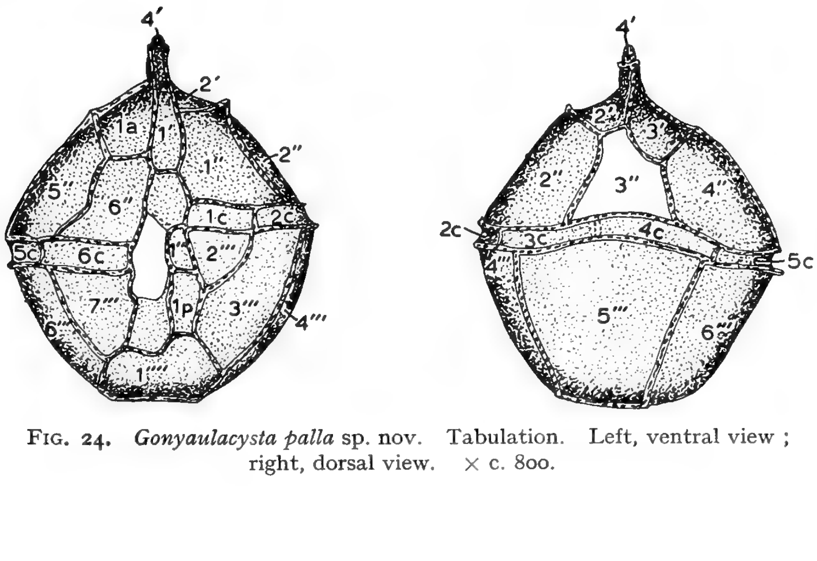


FIG. 24. *Gonyaulacysta palla* sp. nov. Tabulation. Left, ventral view ; right, dorsal view. × c. 800.

DESCRIPTION. Theca spherical, relatively thin-walled and apparently fragile; of some 20 specimens seen, all had suffered damage additional to archaeopyle formation. The holotype is the best-preserved, but nonetheless shows a tear in median ventral position. Surface densely granular, the granulation rendering the low crests difficult to distinguish in lateral positions.

Apical horn slender and relatively long, accounting for about $\frac{1}{6}$th of the thecal length. Its tip is formed by plate 4′, its base by plates 1 to 3′. Six precingular plates, with plate 6′ reduced to accommodate the anterior intercalary plate. Either six or seven postcingular plates; presence of the presumed boundary between plates 4″ and 5″ could not be completely verified in any specimen seen, through a combination of damage and unfortunate orientation. Plates 1‴ and 1p are both small: plate 2‴ is also reduced and does not have a boundary with the antapical plate. The antapical plate has the appearance of being inclined towards the ventral face, but this may simply result from compression.

The cingulum is of moderate breadth and strongly laevorotatory, its two ends differing in antero-posterior position by about one and a half times its breadth. The number of cingular plates is doubtful. The sulcus is short and of moderate breadth.

All specimens seen have a precingular archaeopyle, formed by loss of plate 3″.

REMARKS. In its combination of overall morphology and tabulation, *Gonyaulacysta palla* differs from all other described species. The most closely similar species is *G. ambigua* (Deflandre), which has a similarly spherical shape and crests of comparable character, but differs in having no comparable apical horn and a different ventral tabulation.

Gonyaulacysta axicerastes sp. nov.

Pl. 13, figs. 11, 12; Text-fig. 25

DERIVATION OF NAME. Greek, *axon*, axis; *kerastes*, horned—hence, axially horned.

DIAGNOSIS. A *Gonyaulacysta* having a spheroidal shell with apical pericoel crowned by slender horn arising from periphragm. Second short horn, formed from both membranes, present at antapex. Tabulation ?4′, 1a, 6″, 6c, 6‴, 1p, 1⁗; plate boundaries bearing high delicate crests. Cingulum and sulcus relatively narrow, sulcus somewhat sinuous and broadening posteriorly.

HOLOTYPE. B.M.(N.H.) slide V.51727(1). Speeton Clay, Shell West Heslerton Borehole No. 1, West Heslerton, Yorks., at 39 metres depth. Lower Cretaceous (Middle Barremian).

DIMENSIONS. Holotype: overall length 71μ, breadth 60μ; shell length 50μ, breadth 52μ; width of cingulum c.5μ; length of apical horn, 8μ; length of antapical horn, 7·5μ. Other specimens seen too damaged for measurement.

DESCRIPTION. Shell spheroidal, slightly broader than long, with epitract surmounted by a dome-like outgrowth of the periphragm enclosing an apical pericoel. A slender, furcate horn arises from the apex. The dome-like structure arises from the confluent crests of the plates on the apical portion of the epitract ; position of three –? four apical plates and an anterior intercalary plate are indicated by dimples in this structure. Six precingular plates are present, plate 6″ being of reduced size. Six postcingular plates are likewise present, with plate 1‴ slightly reduced to accommodate the posterior intercalary plate. A polygonal plate occupies the antapex ; from its centre arises a short, blunt antapical process. Slender spines at the angles sustain the crests surrounding the antapex ; these crests are not connected to the antapical process.

The cingulum forms a strong laevorotatory spiral such that its two ends differ in antero-posterior position by more than twice its width. It is divided into six cingular plates. The sulcus is sinuous rather than sigmoidal : a median section along its line would touch the two ends of the cingulum but would not cut them. It is of moderate breadth in its epitractal portion, but widens as it approaches the antapex.

The crests are high and delicate, with denticulate edges ; they are irregularly perforate, the perforations being so fine as to be almost imperceptible at high magnifications (× 1,000). The surface bears an irregular, sparse scatter of coarse tubercles, but is otherwise smooth.

No archaeopyle has been observed.

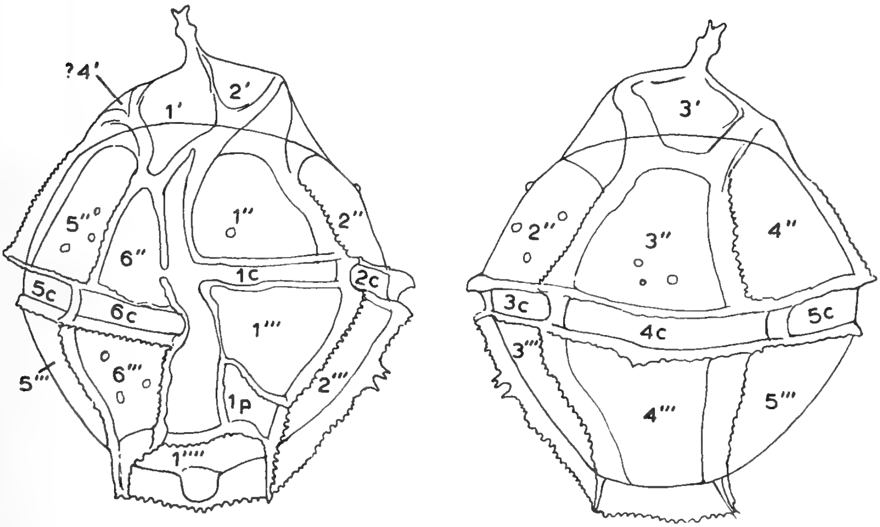


FIG. 25. *Gonyaulacysta axicerastes* sp. nov. Tabulation. Left, ventral view ; right, dorsal view. × c. 1000.

REMARKS. In its possession of an apical pericoel, surmounted by a horn, *Gonyaulacysta axicerastes* differs from all other species of the genus except *G. cassidata*. It differs from *G. cassidata* in the form of the central shell, which is more ovoid in the latter species ; the less markedly sigmoidal form of the cingulum ; the more slender shape of the apical horn ; the detail of ventral tabulation ; and the possession of an antapical horn. *Scriniodinium apaletum* Cookson & Eisenack 1960, from the Upper Jurassic of Australia, has an apical horn and pericoel of similar form but differs in having an antapical pericoel also. The tabulation of *Scriniodinium apaletum* has not yet been fully described.

Gonyaulacysta helicoidea (Eisenack & Cookson)

Pl. 13, figs. 7, 8 ; Pl. 15, figs. 8, 9 ; Text-fig. 26

1960. *Gonyaulax helicoidea* Eisenack & Cookson : 2, pl. 1. figs. 4–9.

EMENDED DIAGNOSIS. A *Gonyaulacysta* with spheroidal to ovoidal theca surmounted by blunt apical horn. Epitract longer than hypotract ; antapex flattened. Tabulation : 4′, 1a, 6″, 6c, 6‴, 1p, ?1 p.v., 1⁗ ; plates bordered by denticulate crests, varying considerably both in height and character of denticulation. Cingulum strongly spiral : sulcus sigmoidal, plates 6″ and 1‴ roughly L-shaped. Surface bearing irregular scatter of tubercles.

HOLOTYPE. The specimen figured by Eisenack & Cookson (1960, pl. 1, fig. 4). I. C. Cookson Colln., Melbourne. Lower Cretaceous (Aptian or older) ; Lake Phillipson bore, South Australia, at 87 ft. 10 in.

MATERIAL (figured). B.M.(N.H.) slide V.51718(1), Speeton Clay, Shell West Heslerton Borehole No. 1, West Heslerton, Yorks., at 42·5 metres depth, Lower Cretaceous (Lower Barremian).

DIMENSIONS. Holotype : overall length 78μ, breadth 56μ. Range of Australian specimens : overall length 62–86μ, breadth 48–67μ. Figured specimen (Speeton Clay) : overall length 45μ, breadth 45μ ; shell length 38μ, breadth 43μ ; length of horn 7μ. Range of English specimens : overall length 44–53μ, breadth 42–46μ.

DESCRIPTION. The shell shape varies from an ovoid to an oblate spheroid ; the length of the horn and the height and form of the crests are also very variable.

Of the four apical plates, plate 1′ occupies the anterior prolongation of the sulcus : it is long and narrow. An elongate anterior intercalary plate is present alongside it. The four apical plates together form the apical horn, their crests being confluent at its tip. Six precingular plates are present, with plate 6″ small, elongate, and roughly L-shaped. Six post-equatorial plates are present, plate 1‴ being roughly axe-shaped, with broad anterior and narrow posterior portions. A quadrate posterior

intercalary plate is present. The single antapical plate is large and polygonal ; the crests surrounding it are supported at their junctions by spines. A posterior ventral plate may be present, but if so, its anterior boundary is ill-defined.

The cingulum is relatively narrow and pronouncedly laevo-rotatory, its two ends differing in antero-posterior position by three times its width. The sulcus is markedly sigmoidal ; a median dorso-ventral section would thus cut both ends of the cingulum. Six cingular plates appear to be present ; the posterior end of the cingulum is separated from the sulcus by a small crescentic plate, poorly marked or indistinguishable in many specimens and thus excluded from the diagnosis. The crests crossing furrows lack denticles.

An irregular scatter of tubercles is present on the surfaces of the plates ; the number, density and situation of these tubercles varies greatly between individuals.

A precingular archaeopyle is usually present, formed by loss of plate 3″.

REMARKS. The diagnosis of *Gonyaulacysta helicoidea* is emended to include reference to the tabulation. This species is numerous in the assemblages from 39 and 42·5 metres depth in the Speeton Clay ; although the English specimens are markedly smaller, there can be no doubt that they are conspecific with the Australian species.

A closely comparable species, *Gonyaulacysta cretacea* (Neale & Sarjeant 1962) is present in somewhat earlier horizons (99·25 metres—Hauterivian) in the West Heslerton boring. This differs from *G. helicoidea* only in having a more markedly polygonal outline and in lacking tubercles. It seems probable that *G. cretacea* is ancestral to *G. helicoidea*.

The form from the Lower Cretaceous of New South Wales, figured by Deflandre & Cookson (1956, pl. 1, fig. 6) as ?*Gonyaulax* sp. indet., may well be attributable to this species.

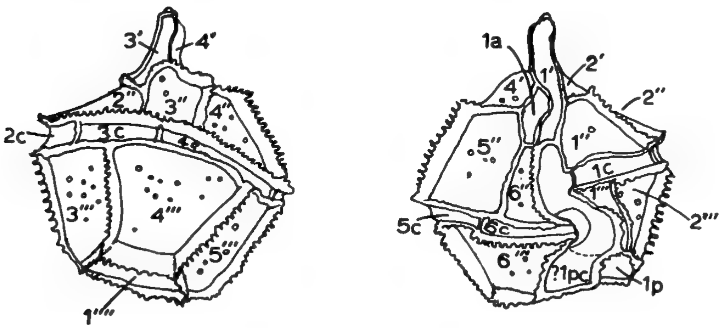


FIG. 26. *Gonyaulacysta helicoidea* (Eisenack & Cookson). Tabulation. Left, ventral view ; right, dorsal view. × c. 800.

Gonyaulacysta episoma sp. nov.

Pl. 13, figs. 9, 10 ; Text-fig. 27

DERIVATION OF NAME. Greek, *episomos*, bulky, fat—referring to the rotund shell shape.

DIAGNOSIS. A *Gonyaulacysta* with spherical to broadly ovoid shell with strong apical horn of moderate length. Tabulation 4′, 1a, 6″, ?5c, 6‴, 1p, 1 p.v., 1⁗. Crests consisting of rows of thin spinelets connected distally by trabeculum ; an extremely delicate membrane stretching between spinelets and trabecula. Cingulum strongly spiral ; sulcus broad and short, stretching from about mid-point on epitheca to about mid-point on hypotheca. Surface densely granular ; very few spines occasionally present. Horn with trifurcate appearance produced by high crest bounding plate 4′.

HOLOTYPE. B.M.(N.H.) slide V.51730(1). Speeton Clay, Shell West Heslerton Borehole No. 1, West Heslerton, Yorks., at 19·25 metres depth, Lower Cretaceous (Upper Barremian).

DIMENSIONS. Holotype : overall length 80μ, breadth 74μ ; shell length 70μ, breadth 68μ ; horn 10μ in length ; crests c.2μ in height ; cingulum c.3μ broad. Range of dimensions : overall length 80–95μ, horn length 10–18μ, breadth 60–80μ.

DESCRIPTION. An abundant species at this horizon, some 30 specimens having been examined. All show some degree of distortion as a result of compression of the originally spherical, fairly thin-walled shell. The horn is short, strongly tapering and pointed ; it is tipped by plate 4′, the high crest bounding this plate producing a

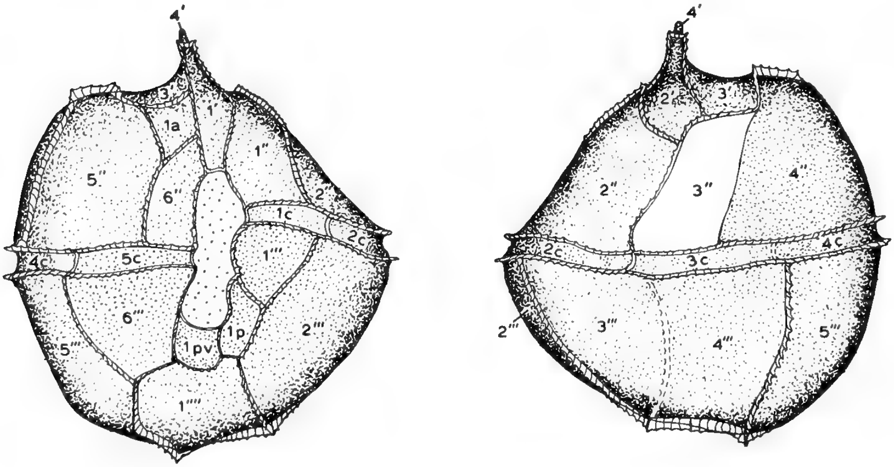


FIG. 27. *Gonyaulacysta episoma* sp. nov. Tabulation. Left, ventral view ; right, dorsal view. × c. 800.

characteristic trifurcate appearance. There are four apical plates, plate 1′ occupying the anterior prolongation of the sulcus and being unusually broad. Six precingular plates are present, the sixth being reduced to accommodate the anterior intercalary plate.

Six postcingular plates are present, plate 1‴ being reduced to accommodate the posterior intercalary plate. A roughly quadrate posterior ventral plate separates the sulcus from the single large antapical plate.

The cingulum is of moderate breadth and forms a strong laevorotatory spiral such that its two ends differ in antero-posterior position by three times its breadth. It comprises cetainly five, possibly six cingular plates. The sulcus is short and broad.

The surface is densely granular. In at least one specimen (figured), a very few short spines are present on the surface of the hypotract : spines are not present, however, on the holotype. The degree of granulation of the sulcus is markedly less than that of the rest of the surface.

A precingular archaeopyle, formed by loss of plate 3″, is present in all specimens seen.

REMARKS. *Gonyaulacysta episoma* sp. nov. is characterized by its combination of shape, tabulation and crest character. *Gonyaulacysta nuciformis* (Deflandre 1938), from the Upper Jurassic, has a somewhat similar overall shape and degree of granulation, but the shell wall is thicker, the tabulation is less clear and the form of the crests is quite different. *Gonyaulacysta scotti* (Cookson & Eisenack 1958) an inadequately described species from the Upper Jurassic of Western Australia, has rather similar crests, but has a more markedly ovoidal shape and an apical horn of dissimilar type. *Gonyaulacysta tenuiceras* (Eisenack 1958) from the Aptian of Germany, has a horn and crests of somewhat similar character, but the crests are much higher and the tabulation is markedly different. A specimen figured as *G. tenuiceras* by Alberti (1961, pl. 11, fig. 7), from the Upper Barremian of Germany, may well be in fact *G. episoma*.

Gonyaulacysta hadra sp. nov.

Pl. 14, fig. 1 ; Text-fig. 28

DERIVATION OF NAME. Greek, *hadros*, well-developed, bulky, stout—referring to the unusually large size.

DIAGNOSIS. A *Gonyaulacysta* with thick-walled, spherical to spheroidal shell and long, tapering apical horn. Tabulation 4′, ?oa, 6″, 6c, 6‴, 1p, 1 p.v., 1⁗ ; poorly marked by crests in form of very low ridges bearing well spaced, extremely abbreviate spinelets. Cingulum weakly spiral : sulcus short, confined to ventral region. Surface generally densely granular.

HOLOTYPE. B.M.(N.H.) slide V.51731(1). Speeton Clay, Shell West Heslerton No. 1 Borehole at 19·25 metres depth, West Heslerton, Yorks., Lower Cretaceous (Upper Barremian).

PARATYPE. B.M.(N.H.) slide V.51730(5). Same locality and horizon.

DIMENSIONS. Holotype : overall length 151μ, breadth 117μ. Shell length 117μ ; length of horn 34μ ; breadth of cingulum c.7μ. Paratype : overall length 145μ, breadth c.112μ ; shell length 105μ ; length of horn 40μ ; breadth of cingulum c.5μ. Range : overall length c.140–155μ.

DESCRIPTION. This is an unusually large and very characteristic species, quite frequent at this horizon, some 20 specimens having been studied. The dense granulation and relatively inconspicuous character of the crests render the tabulation difficult to determine : Text-fig. 28 was prepared from study of several specimens and is unlikely to be accurate in detail. On most specimens, including the holotype, granules are absent from various small patches of the surface : this appears to result from damage. Granulation is consistently faint or lacking on the sulcus, which is somewhat sunken.

The test is spherical to spheroidal and composed of two distinct layers ; a fairly thin periphragm and a thicker endophragm. The endophragm bulges only into the base of the apical horn, so that the horn contains a cavity between the wall layers.

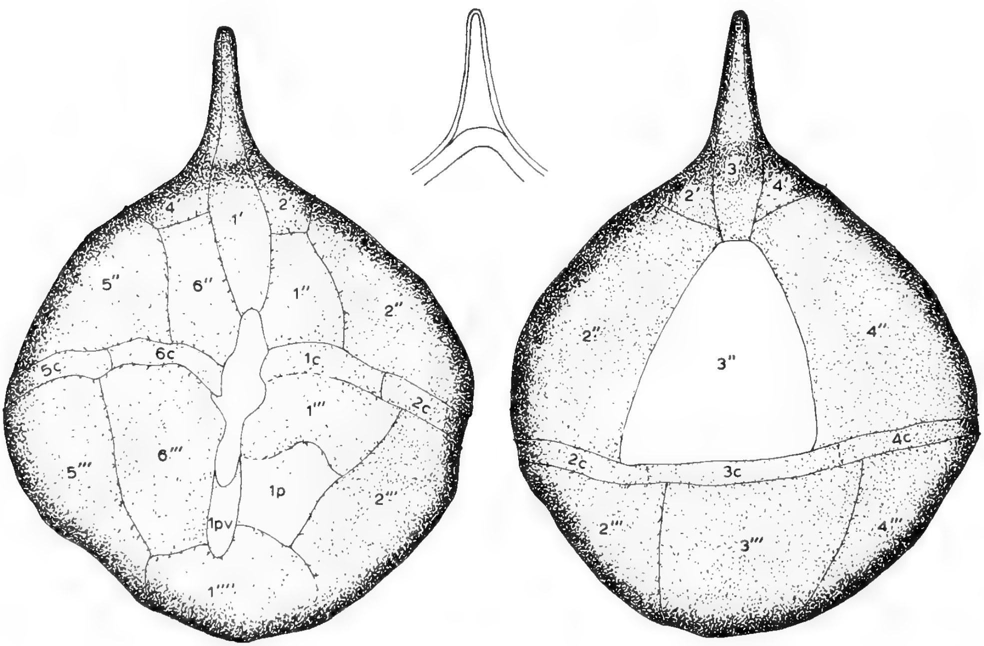


FIG. 28. *Gonyaulacysta hadra* sp. nov. Tabulation. Left, ventral view ; right, dorsal view. Insert : the wall structure at the apex, in diagrammatic section. × c. 550.

Four apical plates are present, jointly forming the apical horn. Plate 1′ is long and broad, occupying the anterior prolongation of the sulcus. An anterior intercalary plate could not be determined. Six precingular plates are present, plates 1″ and 6″ being reduced. There are also six postcingular plates, with plate 1‴ reduced to accommodate the large posterior intercalary plate. A narrow posterior ventral plate separates the polygonal antapical plate from the sulcus.

The cingulum forms a feebly laevorotatory spiral, its two ends scarcely differing in antero-posterior position. The sulcus is short, extending only over the middle third of the ventral surface : it is widest at mid-point and tapers to anterior and posterior.

A precingular archaeopyle, formed by loss of plate 3″, is present in all specimens seen.

REMARKS. In general form, tabulation and crest character, *Gonyaulacysta hadra* sp. nov. differs from all described species.

Gonyaulacysta orthoceras (Eisenack)

Pl. 14, figs. 5, 6 ; Text-fig. 29

1958. *Gonyaulax orthoceras* Eisenack : 388, pl. 21, figs. 3–14, pl. 24, fig. 1. ; text-figs. 2, 3.
1959. *Gonyaulax orthoceras* Eisenack ; Gocht : 54, pl. 5, figs. 12, 13.
1961. *Gonyaulax orthoceras* Eisenack : Alberti : 6, pl. 11, figs. 1–3.
1963. *Gonyaulax orthoceras* Eisenack ; Górka : 30, pl. 3, figs. 1–4.

EMENDED DIAGNOSIS. A *Gonyaulacysta* having an ovoidal theca of moderate wall thickness, with strong, tapering apical horn accounting for about one-fifth to one quarter of overall length. Tabulation 4′, 1a, 6″, ?6c, 7‴, 1p, 1⁗ ; plate boundaries outlined by low crests bearing very abbreviate spinelets. Cingulum strongly spiral, of moderate breadth : sulcus broad and extending to antapex. Surface of shell granular to tuberculate.

HOLOTYPE. The specimen illustrated by Eisenack (1958, pl. 21, fig. 5) from Preparation Ob. Apt. no. 32. Aptian glauconitic limestone, Deutschen Erdol A.G., Erdolwerke Holstein, boring Marne, Feld Heide, North Germany, at 761–7 metres depth.

MATERIAL (figured). B.M.(N.H.) slide V.51730(3). Speeton Clay, Shell West Heslerton Borehole No. 1, West Heslerton, Yorks., at 19·25 metres depth. Lower Cretaceous (Upper Barremian).

DIMENSIONS. Holotype : overall length 95μ, breadth 71μ ; length of horn 22μ. Range of German specimens : overall length 70–105μ. Figured specimen : overall length 100μ, breadth 80μ ; length of horn c.20μ ; width of cingulum c.5μ. Range of English specimens ; overall length 80–115μ.

DESCRIPTION. Shell broadly ovoidal, with the hypotract rounded. The crests separating the four apical plates converge at the apex. Plate 1′ occupies the anterior prolongation of the sulcus and is markedly elongate. Six precingular plates are present, with plate 6″ very reduced to accommodate an anterior intercalary plate. Seven postcingular plates are present, plates 1‴ and 2‴ being reduced to accommodate a rather indistinctly demarcated posterior intercalary plate. A single polygonal plate occupies the antapex.

The cingulum forms a laevorotatory spiral such that its two ends differ in antero-posterior position by over three times its width. The number of cingular plates appears to be six, but the crests separating them are poorly marked. The sulcus is of moderate breadth and extends from mid-point on the epitract to the antapex.

The shell wall is of moderate thickness and consists of two distinct layers. The apical horn is formed by the periphragm, the endophragm showing no outbulge; the horn is thus hollow and contains what is effectively an apical pericoel. The English specimens have a densely granular surface, but lack tubercles such as are present on the German specimens.

A precingular archaeopyle, formed by loss of plate 3″, is generally present.

REMARKS. The diagnosis is emended to include reference to the tabulation. In his original diagnosis, Eisenack figures two alternative tabulation patterns and

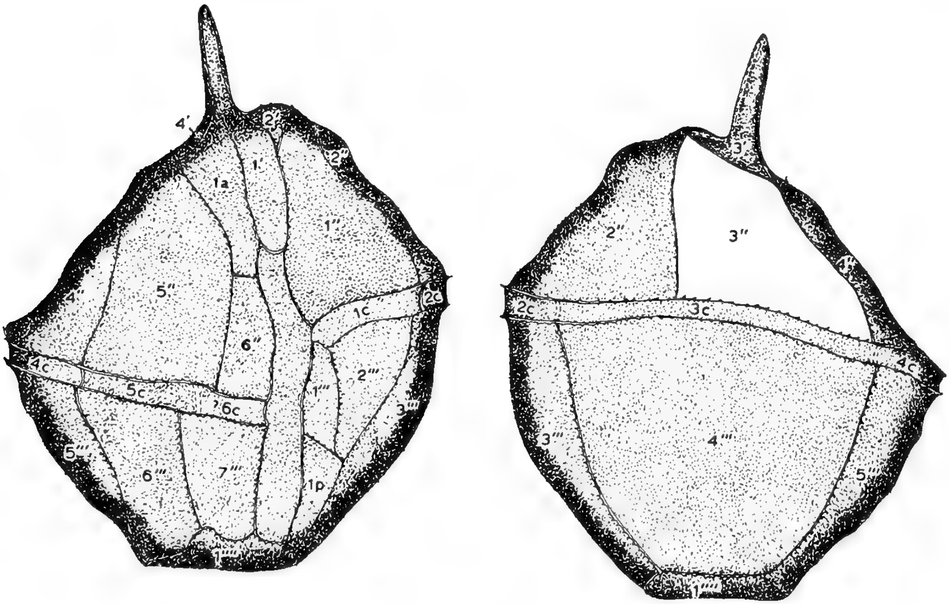


FIG. 29. *Gonyaulacysta orthoceras* (Eisenack). Tabulation. Left, ventral view; right, dorsal view. × c. 750.

expresses doubt as to which is correct ; he comments on the difficulty of distinguishing crests from folds. The tabulation presented in Eisenack's Text-fig. 3 agrees closely with that determined from the English specimens. The plate here designated as postcingular plate 1''' is figured, but not numbered ; Eisenack's plates 1''' to 6''' thus correspond to plates 2''' to 7''' of the scheme here adopted. The presence of anterior and posterior intercalary plates is confirmed.

Gonyaulacysta orthoceras (Eisenack 1958) is an abundant and characteristic Cretaceous species, having a known range from Upper Valanginian to Turonian. It is clearly distinguishable through its combination of shape, tabulation, and nature of crests : comparisons with other described species are discussed by Eisenack (1958 : 389) and Górka (1963 : 31).

Gonyaulacysta aichmetes sp. nov.

Pl. 13, figs. 5, 6 ; Text-fig. 30

DERIVATION OF NAME. Greek, *aichmetes*, spearman, warrior ; referring to the pronounced apical horn.

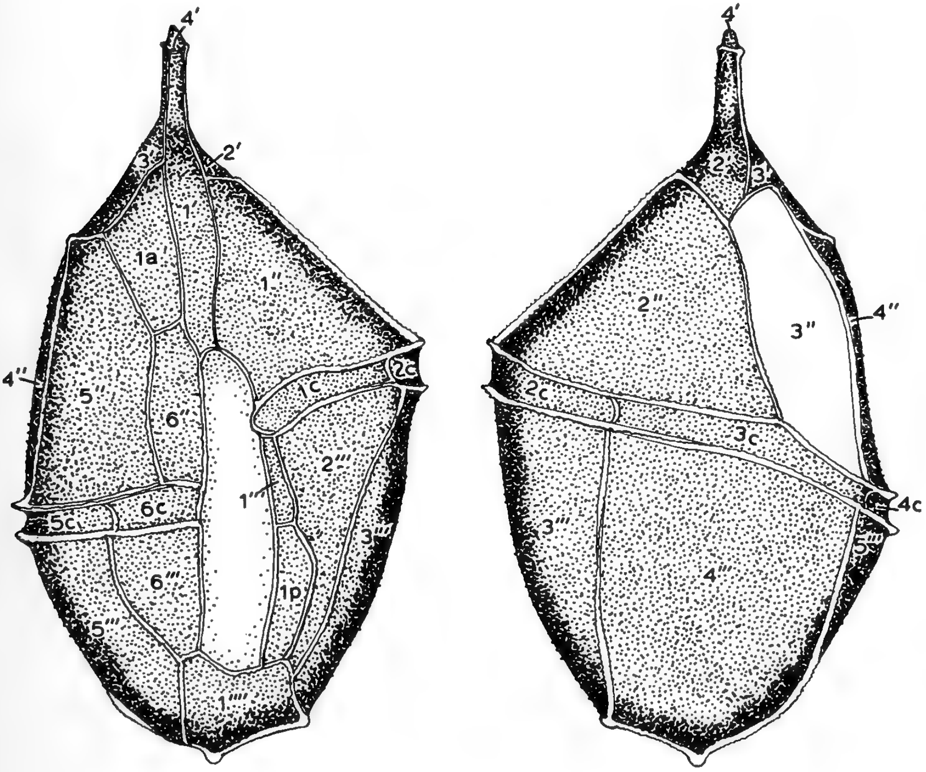


FIG. 30. *Gonyaulacysta aichmetes* sp. nov. Tabulation. Left, ventral view ; right, dorsal view. × c. 1000.

DIAGNOSIS. A *Gonyaulacysta* with ovoidal to broadly ellipsoidal theca and strong, tapering apical horn accounting for about one-sixth to one-seventh of overall length. Tabulation 4′, 1a, 6″, 6c, 6‴, 1p, 1⁗. Crests delimiting plates represented by low ridges, minutely serrate ; those bordering cingulum higher. Cingulum strongly spiral, of moderate breadth ; sulcus sunken, broad, with only short epitractal section. Surface of shell densely granular ; granulation less pronounced on sulcus.

HOLOTYPE. B.M.(N.H.) slide V.51730(2). Speeton Clay, Shell West Heslerton Borehole No. 1, West Heslerton, Yorks., at 19·25 metres depth. Lower Cretaceous (Upper Barremian).

DIMENSIONS. Holotype : overall length 101μ, breadth 64μ (minimum) ; shell length 84μ, breadth 56μ (minimum) ; length of horn, 16μ ; width of cingulum c.4·5μ. Range of dimensions : overall length c.95–105μ, breadth c.55–65μ.

DESCRIPTION. This is a relatively infrequent species, some 6 specimens only having been studied. The holotype was the best oriented for study, but is somewhat crushed in at right, so that breadth measurements stated are minima and the right-hand tabulation is possibly inaccurate, albeit confirmed in some measure by study of other specimens.

There are four apical plates ; the apical horn is tipped by plate 4′, its flanks being formed by the other three plates. Plate 1′ is especially elongate, extending down almost two-thirds of the epitract. Six precingular plates are present, plate 6″ being reduced to accommodate a very large anterior intercalary plate. Six post-cingular plates are present, with plate 1‴ reduced and very elongate ; an elongate posterior intercalary plate lies between it and the antapex. A single, rather quadrate plate occupies the antapex.

The cingulum forms a strong laevorotatory spiral such that its two ends differ in antero-posterior position by twice its width. It is bordered by strong ridges. The cingular plates are poorly defined, but appear to be six in number. The sulcus is broad and relatively short, extending to the antapex.

The shell surface is densely granular. The crests are low but generally readily perceptible : they are finely but irregularly serrate.

A precingular pylome, formed by loss of plate 3″, is present in all specimens seen.

REMARKS. *Gonyaulacysta aichmetes* sp. nov. is of a general form similar to several other Cretaceous species, but is distinguished by shape, crest character and detail of the tabulation. The most comparable species is undoubtedly *Gonyaulacysta apionis* (Cookson & Eisenack 1958) from the Albian of South Australia. However, this latter species has a more ellipsoidal shape, smooth crests and four pronounced projections bordering the antapical plate ; its tabulation has not been fully specified, but, from the figures given (Cookson & Eisenack 1958, text-figs. 3, 4) plate 1 appears to be less elongate, there appears o be no anterior intercalary plate, and the posterior ventral structure appears different. The " lid " on the apical horn of *G. apionis* is probably simply a small apical plate edged by crests, such as is present in *G. aichmetes*.

Gonyaulacysta cassidata (Eisenack & Cookson)

Pl. 14, figs. 3, 4 ; Text-fig. 31

1960. *Gonyaulax helicoidea* subsp. *cassidata* Eisenack & Cookson : 3, pl. 1, figs. 5, 6.
1962. *Gonyaulax cassidata* Eisenack & Cookson ; Cookson & Eisenack : 486, pl. 2, figs. 1, 2.
1964. *Gonyaulax cassidata* Eisenack & Cookson ; Cookson & Hughes : 42, pl. 5, fig. 10 only.

EMENDED DIAGNOSIS. A *Gonyaulacysta* with thin-walled, broadly ovoidal theca, surmounted by apical pericoel terminating in short horn. Tabulation 4', 1a, 6", 6c, 6''', 1p, 1'''' ; plate boundaries demarcated by high, delicate crests with smooth or denticulate edges. Cingulum strongly spiral, of moderate breadth : sulcus broadening posteriorly, weakly sigmoidal. (A median dorso-ventral plane would barely intersect the two ends of the cingulum.) Surface of shell smooth or only minutely granular : irregular scatter of tubercles present in some specimens.

HOLOTYPE. Specimen P.17869, National Museum of Victoria, Australia. Lower Cretaceous (Albian) ; Santos's Oodnadatta bore, South Australia, at 327 feet depth.

MATERIAL (figured). Geol. Surv. Colln. slide PF.3047(1). Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey, at 730 feet depth. Upper Cretaceous (Cenomanian).

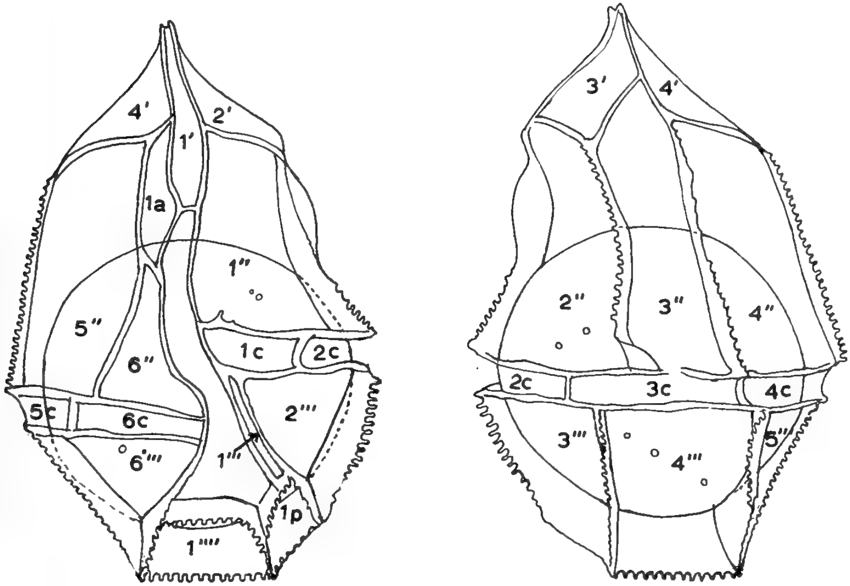


FIG. 31. *Gonyaulacysta cassidata* (Eisenack & Cookson). Tabulation. **Left,** ventral view ; right, dorsal view. × c. 1000.

DIMENSIONS. Holotype : overall length 83μ, breadth 52μ. Range of Australian specimens : overall lengths 71 to 95μ, breadths 47 to 57μ. Figured specimen : overall length 78μ, breadth 53μ, shell length 42μ, breadth 45μ. Range of English specimens : overall lengths 60 to 78μ breadths 46 to 53μ.

DESCRIPTION. Shell broadly ovoidal, the apical pericoel and high antapical crests imparting a polygonal appearance. The crests separating the four apical plates converge at the top of the apical horn, which has a bifid appearance. Plate 1′ is elongate but relatively short, occupying the anterior prolongation of the sulcus. The apical pericoel comprises the apical plates, the anterior intercalary plate and the anterior portions of the six precingular plates : its volume is between one-third and two-thirds that of the shell proper, The anterior plate is somewhat elongate : plate 6″ is reduced and almost triangular. Six postcingular plates are present. Plate 1‴ is reduced and linear, difficult to see in many specimens : it is displaced by the posterior broadening of the sulcus. A small, quadrate posterior intercalary plate separates plates 1‴ and 2‴ from the single, polygonal antapical plate.

The cingulum forms a laevo-rotatory spiral such that its two ends differ in antero posterior position by over twice its width. It is composed of six plates. The sulcus is of moderate breadth on the epitract but broadens considerably as it approaches the antapex.

The shell wall and the crests are both delicate. The crests are high, typically but not consistently denticulate, sometimes minutely and irregularly perforate : the very high crests surrounding the antapex appear to be sustained by delicate spines at the angles. Tubercles may be present ; their number and distribution varies considerably between individuals.

A precingular archaeopyle is formed by loss of plate 3″ : in some specimens, including the figured specimen, the cingulum is slightly torn also.

REMARKS. The diagnosis is emended to include reference to the tabulation. The English specimens correspond closely to those figured from Australia, differing only in details of shape and proportionate size of shell and pericoel, features in which some degree of variation would be expected.

Cookson & Hughes (1964) described this species from the Cambridge Greensand (?Albian–basal Cenomanian) : of two forms figured, one (p. 5, fig. 10) corresponds to *Gonyaulacysta cassidata* as here interpreted, the other (p. 5, fig. 11) appears to belong to *Psaligonyaulax deflandrei* sp. nov. (p. 137). Both species range right through the Cenomanian horizons of the Chalk of the Fetcham Mill Borehole, albeit consistently in low numbers only.

Gonyaulacysta whitei sp. nov.

Pl. 14, fig. 2 ; Text-fig. 32

DERIVATION OF NAME. Named in honour of two early workers on fossil micro-plankton—Henry Hopley White of Clapham, England, an amateur microscopist

who described assemblages from the Chalk in 1842–44, and M. C. White of the United States, who described in 1862 the first Palaeozoic assemblages, from New York State.

DIAGNOSIS. A *Gonyaulacysta* having an ovoidal theca with short, blunt apical horn formed from both shell layers. Tabulation 3′, 1a, 6″, 6c, 6‴, 1p, 1⁗ : plate boundaries demarcated by moderately high crests, densely and finely perforate, with straight or ragged edges. Cingulum broad, strongly spiral : sulcus sigmoidal, of moderate breadth but widening somewhat posteriorly. (A median dorso-ventral plane would barely intersect the two ends of the sulcus.) Surface of shell smooth or only very minutely granular. Crests bounding antapex supported at the angles by strong, broad spines.

HOLOTYPE. Geol. Surv. Colln. slide PF.3048(1), Chalk. H.M. Geological Survey Borehole, Fetcham Mill, Surrey at 770 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype : overall length 62μ, breadth 49μ : shell length 53μ, breadth 45·5 ; length of horn 9μ.

DESCRIPTION. Shell rotund, lemon-shaped, the apical horn joining the shell so smoothly as to have no precise base. Only three apical plates, the crests bounding them forming a pimple on the tip of the apical horn. Plate 1′ is elongate and occupies the anterior prolongation of the sulcus : its posterior boundary was not clearly determined. An anterior intercalary plate and six precingular plates are present, plate 6″ being reduced and subtriangular. Six postcingular plates are present, plate 1‴ being very small and having an ill-defined boundary with the sulcus. The single posterior intercalary plate separates plates 1‴ and 2‴ from the quadrate antapical plate.

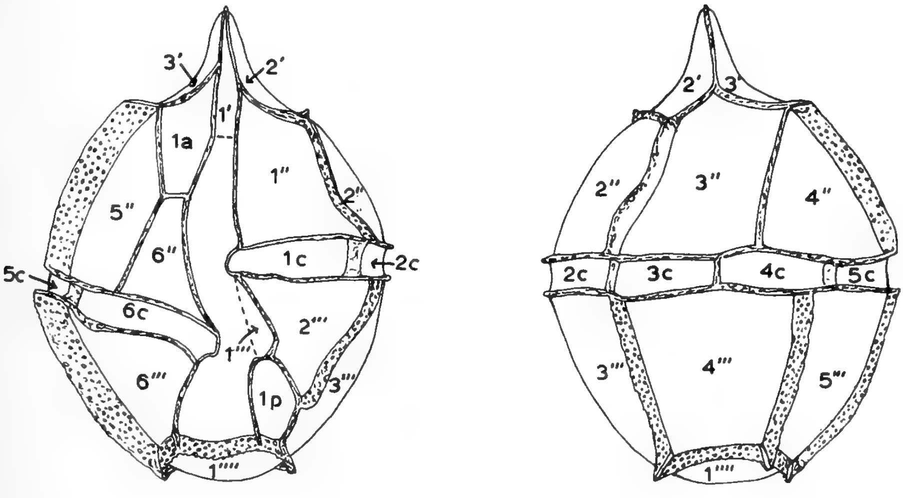


FIG. 32. *Gonyaulacysta whitei* sp. nov. Tabulation. Left, ventral view ; right, dorsal view. × c. 1000.

The cingulum forms a laevorotatory spiral such that its two ends differ in antero-posterior position by almost 4 times its breadth. Six cingular plates are present : the ends of plates 1c and 6c extend somewhat into the sulcus. The epitractal portion of the sulcus is of moderate breadth ; the hypotractal portion broadens progressively as it approaches the antapex.

A precingular archaeopyle is formed by loss of plate 3″.

Remarks. This species is based on a single specimen, well preserved and displayed : its characters are considered sufficiently distinctive to justify creation of a new species. Shape, tabulation and crest character distinguish *Gonyaulacysta whitei* sp. nov. from all other described species.

Gonyaulacysta fetchamensis sp. nov.

Pl. 15, figs. 1, 2 ; Text-fig. 33

Derivation of name. Refers to the type locality, Fetcham Mill, Surrey.

Diagnosis. A *Gonyaulacysta* having an ovoidal theca with strong, blunt apical horn formed by periphragm only. Tabulation 3–?4′, 1a, 6″, 6c, 7‴, 2p, 1⁗ ; sutures in form of low but well-marked, rather fibrous crests giving rise occasionally to short, blunt spines. Cingulum narrow, strongly spiral ; sulcus broad, sunken. Shell surface densely granular.

Holotype. Geol. Surv. Colln. slide PF.3046(1). Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey, at 840 feet depth. Upper Cretaceous (basal Cenomanian).

Dimensions. Holotype : overall length 125μ, breadth 108μ ; shell length 95μ, breadth 98μ ; length of horn c.25μ.

Description. This species is extremely infrequent : of three specimens encountered, one (the holotype) is well preserved, the other two are severely damaged.

The shell is broadly ovoidal, giving rise to a strong, blunt apical horn; this horn is formed by the periphragm only and constitutes what is effectively an apical pericoel. There are certainly three and possibly four apical plates, presence of a crest separating plates 3′ and 4′ being unconfirmed. Plate 1′ is unusually large and club-shaped. Six precingular plates are present, with plate 6″ reduced to accommodate a subtriangular anterior intercalary plate. Seven postcingular plates are present. Plates 1‴ and 2‴ are reduced to accommodate a large posterior intercalary plate, and plate 7‴ is also reduced to accommodate a second, smaller intercalary plate. (The crest separating plates 5‴ and 6‴ is somewhat torn.) The antapex is occupied by a single plate of moderate size.

The cingulum is narrow, forming a laevorotatory spiral such that its two ends differ in antero-posterior position by almost three times its width. The ends of the cingulum are widely separated by a very broad sulcus, which widens further in its posterior portion.

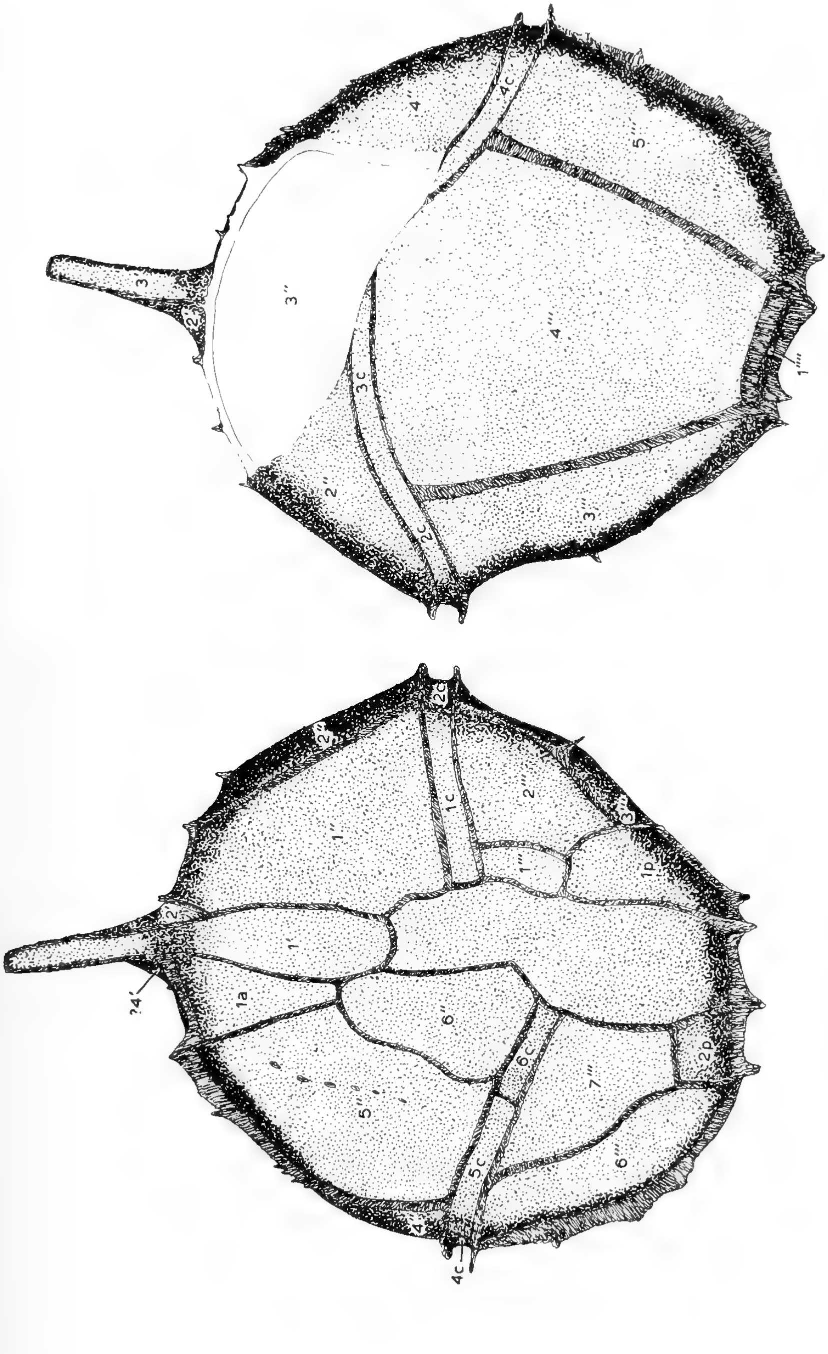


FIG. 33. *Gonyaulacysta fetchamense* sp. nov. Tabulation. Left, ventral view; right, dorsal view. × c. 800.

The crests are fibrous in nature, with close-set slits in places : they give rise to occasional short spines. In the holotype a broken line of " tubercles ", like an embryonic crest, crosses plate 5″ ; this was not observed in the other specimens.

A precingular archaeopyle is formed by loss of the large plate 3″. In the holotype, the region round the archaeopyle is somewhat folded.

REMARKS. The generic allocation of *Gonyaulacysta fetchamensis* is questionable, in view of its possession of two posterior intercalary plates and a seventh postcingular plate. The similarity in general morphology to a number of Lower Cretaceous species of *Gonyaulacysta* resulted in its allocation to that genus ; however, it may subsequently prove preferable to erect a new genus for species having this tabulation pattern, a procedure not now adopted in view of the low numbers of specimens encountered to date.

The most closely comparable species is undoubtedly *Gonyaulacysta orthoceras* (Eisenack), which has a similar general form and apical horn. However, *Gonyaulax fetchamensis* is clearly distinguished by the form of its crests and the detail of ventral tabulation.

OTHER SPECIES

The following species are here attributed to the genus *Gonyaulacysta* on the basis of general structure and formation of an archaeopyle by loss of plate 3″ :

Gonyaulacysta aculeata (Klement 1960). Upper Jurassic (?Oxfordian–Kimmeridgian) ; Germany.

Gonyaulacysta amabilis (Deflandre 1939). Upper Jurassic (Kimmeridgian) ; France.

Gonyaulacysta ambigua (Deflandre 1939). Upper Jurassic (Kimmeridgian) ; France.

Gonyaulacysta apionis (Cookson & Eisenack 1958). Lower Cretaceous (Albian) ; South Australia.

Gonyaulacysta aptiana (Deflandre 1935). Lower Cretaceous (Aptian) ; France (see p. 140).

Gonyaulacysta cladophora (Deflandre 1938). Upper Jurassic (Oxfordian) ; France.

Gonyaulacysta clathrata (Cookson & Eisenack 1960*b*). Upper Jurassic (?Tithonian) ; Western Australia.

Gonyaulacysta crassicornuta (Klement 1960). Upper Jurassic (Kimmeridgian) ; Germany.

Gonyaulacysta cretacea (Neale & Sarjeant 1960). Lower Cretaceous (Hauterivian) ; England.

Gonyaulacysta diaphanis (Cookson & Eisenack 1958). Cretaceous (?Aptian) ; Western Australia.

Gonyaulacysta edwardsi (Cookson & Eisenack 1958). Cretaceous (Aptian–Turonian) ; Australia.

Gonyaulacysta eisenacki (Deflandre 1938). Upper Jurassic (Oxfordian) ; France.

Gonyaulacysta eumorpha (Cookson & Eisenack 1960*b*). Upper Jurassic (Oxfordian –Lower Kimmeridgian) ; Western Australia.

Gonyaulacysta granulata (Klement 1960). Upper Jurassic (Oxfordian–Kimmeridgian) ; Germany.

Gonyaulacysta granuligera (Klement 1960). Upper Jurassic (Kimmeridgian) ; Germany.

Gonyaulacysta hyalodermopsis (Cookson & Eisenack 1958). Lower Cretaceous (?Aptian) ; Western Australia.

Gonyaulacysta margaritifera (Cookson & Eisenack 1960*a*). Upper Cretaceous (Senonian) ; Western Australia.

Gonyaulacysta microceras (Eisenack 1958). Lower Cretaceous (Aptian) ; Germany.

Gonyaulacysta millioudi (Sarjeant 1963*b*, 1965). Upper Jurassic (Oxfordian) ; Switzerland.

Gonyaulacysta muderongensis (Cookson & Eisenack 1958). Lower Cretaceous (Aptian) ; Western Australia.

Gonyaulacysta obscura (Lejeune-Carpentier 1946). Upper Cretaceous ; Belgium.

Gonyaulacysta pachyderma (Deflandre 1938). Upper Jurassic (Oxfordian) ; France.

Gonyaulacysta perforans (Cookson & Eisenack 1958). Upper Jurassic ; Papua.

Gonyaulacysta scarburghensis Sarjeant 1964*b* (= *Gonyaulax areolata* n.n. Sarjeant 1961). Upper Jurassic (Oxfordian) ; England.

Gonyaulacysta scotti (Cookson & Eisenack 1958). Upper Jurassic ; Western Australia.

Gonyaulacysta serrata (Cookson & Eisenack 1958). Upper Jurassic–?Lower Cretaceous ; Papua.

Gonyaulacysta tenuiceras (Eisenack 1958). Lower Cretaceous (Aptian) ; Germany.

Gonyaulacysta wetzeli (Lejeune-Carpentier 1939). Upper Cretaceous ; Belgium.

The following described species are doubtfully included in *Gonyaulacysta* on the basis of general structure but in absence of clear knowledge of the mode of archaeopyle formation.

?*Gonyaulacysta aceras* (Eisenack 1958). Lower Cretaceous (Aptian) ; Germany.

?*Gonyaulacysta cornigera* (Valensi 1953). Middle Jurassic (Bathenian) ; France.

?*Gonyaulacysta freakei* (Sarjeant 1963*b*). Upper Jurassic (Oxfordian) ; England.

?*Gonyaulacysta longicornis* (Downie 1957). Upper Jurassic (Kimmeridgian) ; England.

?*Gonyaulacysta mamillifera* (Deflandre 1939). Upper Jurassic (Kimmeridgian) ; France.

?*Gonyaulacysta nannotrix* (Deflandre 1939). Upper Jurassic (Kimmeridgian); France.

?*Gonyaulacysta nealei* (Sarjeant 1962*b*). Upper Jurassic (Oxfordian); England.

?*Gonyaulacysta nuciformis* (Deflandre 1938). Upper Jurassic (Oxfordian); France.

?*Gonyaulacysta porosa* (Lejeune-Carpentier 1946). Upper Cretaceous; Belgium.

?*Gonyaulacysta transparens* (Sarjeant 1959). Middle Jurassic (Callovian); England.

Genus ***ACANTHOGONYAULAX*** nov.

Derivation of name. Greek, *akantha*, thorn, prickle; a spiny variant of the *Gonyaulax* tabulation type.

Diagnosis. Proximate dinoflagellate cysts, spherical, ellipsoidal, ovoidal or polyhedral, with the tabulation 3–4′, 0–1a, 6″, 6g, 6‴, 1p, 0–1 p.v., 1⁗. Cingulum strongly or weakly helicoid; sulcus generally or constantly extending on to epitract. Apical horn present only infrequently; median and antapical horns lacking. Sutures in form of low ridges bearing rows of spines, simple or furcate, or distinguishable only as rows of spines. Shell bearing general cover of simple or furcate spines, identical to or differing from those on sutures; spines fewer or totally lacking on cingulum and/or sulcus. Length of spines always less than $\frac{1}{4}$ of shell width. Surface smooth, granular, nodose, punctate or reticulate. Precingular archaeopyle formed by loss of plate 3″.

Type species. *Gonyaulax venusta* Klement 1960. Upper Jurassic (Oxfordian to Kimmeridgian); Germany.

Remarks. There are a group of Upper Jurassic species characterized by possession of a dense spine cover, through which a tabulation of *Gonyaulax* type may be determined with varying degrees of difficulty. It is probable that these forms developed into spinous species without tabulation. These species form a coherent group which are considered to merit a separate generic name. *Gonyaulax venusta* is selected as type-species, since it shows the tabulation most clearly.

Forms of *Gonyaulacysta* with a coarsely tubercular surface, such as *G. aculeata* (Klement 1960) may represent a transitional stage to *Acanthogonyaulax*.

The following species accord with the diagnosis of this genus:

Acanthogonyaulax acanthosphaera (Sarjeant 1961) comb. nov., Upper Jurassic (Oxfordian); England.

A. paliuros (Sarjeant 1962*a*) comb. nov. Upper Jurassic (Oxfordian); England.

Genus *HESLERTONIA* nov.

DERIVATION OF NAME. Based on the name West Heslerton, Yorkshire, from which the type species was first described.

DIAGNOSIS. Chorate dinoflagellate cysts, spherical, ellipsoidal, ovoidal or polyhedral, with high sutural crests outlining the tabulation 3–4′, 0–1a, 6″, 6g, 6‴, 1p, 0–1 p.v., 1⁗. Cingulum strongly or weakly helicoid ; sulcus generally but not constantly extending on to epitract. Apical and antapical horns absent. Sutures perforate or imperforate ; their distal edges smooth or denticulate. Crest height exceeds $\frac{1}{4}$ of shell width. Surface smooth, granular, punctate, nodose or reticulate. Precingular archaeopyle formed by loss of plate 3″ ; archaeopyle sometimes absent.

TYPE SPECIES. *Gonyaulax heslertonense* Neale & Sarjeant 1962. Lower Cretaceous (Hauterivian) ; England.

REMARKS. This genus is a chorate equivalent of *Gonyaulacysta*, characterized by its disproportionately high crests.

Heslertonia heslertonensis (Neale & Sarjeant)

1962. *Gonyaulax heslertonense* Neale & Sarjeant : 440, pl. 19, fig. 5, pl. 20, fig. 5 ; text-fig. 1.

REMARKS. Forms closely comparable to this species have been figured and described from the Middle Cretaceous of Australia as *Cymatiosphaera striata* Eisenack & Cookson (1960 : 9, pl. 3, figs. 10, 11). Both forms have in common high, striate crests : the figures suggest that the Australian species also has a cingulum and a determinable tabulation. A full restudy of the Australian specimens appears necessary to determine whether *H. heslertonense* and *C. striata* are congeneric or conspecific; should the latter prove to be the case, the earlier name *striata* would have priority.

Genus *LEPTODINIUM* Klement 1960 : 45

EMENDED DIAGNOSIS. Proximate dinoflagellate cysts, spherical, ovoidal, ellipsoidal or polyhedral, with the tabulation 4′, 6″, 5–?6g, 5‴, 1p, 1⁗. Cingulum strongly or weakly helicoid, sulcus generally but not constantly extending on to epitract, undivided or subdivided into a pattern of ventral plates. Sutures between plates in form of low ridges, or bearing crests of varied form (smooth, denticulate or spinous ; perforate or imperforate). Height of crests always less than $\frac{1}{4}$ of shell width. Surface of shell smooth, granular or punctate. Precingular archaeopyle formed by loss of plate 3″ ; not all individuals may show an archaeopyle.

TYPE SPECIES. *Leptodinium subtile* Klement 1960. Upper Jurassic (Oxfordian to Lower Kimmeridgian) ; Germany.

REMARKS. The diagnosis is emended to include mention of the archaeopyle and more detail of other features. Differentiating features from *Gonyaulacysta* are the smaller number of postcingular plates and the lack of an anterior intercalary plate. A number of species of the latter genus show reduction of the first postcingular plate : presence or absence of an anterior intercalary plate is then determinative.

Leptodinium alectrolophum sp. nov.

Pl. 15, figs. 3–6 ; Text-fig. 34

DERIVATION OF NAME. Greek, *alectrolophos*, cockscomb, in reference to the distinctive crests.

DIAGNOSIS. A *Leptodinium* having an ovoidal theca, without apical horn. Tabulation $4'$, $6''$, 7c, $5'''$, 1p, $1''''$; plate boundaries bearing high, delicate crests which form slight projections at their points of junction. Sulcus and cingulum both of moderate breadth : sulcus relatively long, extending almost from apex to antapex. Cingular plate 7c roughly diamond-shaped. Apical prominence formed by junction of crests of apical plates.

HOLOTYPE. B.M.(N.H.) slide V.51725(1). Speeton Clay, Shell West Heslerton Borehole No. 1., West Heslerton, Yorks., at 39 metres depth. Lower Cretaceous (Middle Barremian).

PARATYPE. V.51725(2). Same locality and horizon.

DIMENSIONS. Holotype : overall length 56μ, breadth 50μ ; shell length 47·5μ, breadth 42·5μ ; width of cingulum c.5·5μ. Paratype : overall length 61·5μ, breadth 54·5μ ; shell length 50μ, breadth 46μ ; width of cingulum c.6μ. Other specimens observed were of intermediate dimensions.

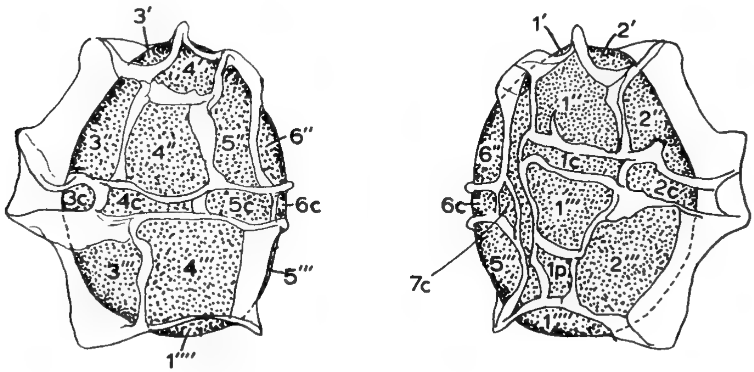


FIG. 34. *Leptodinium alectrolophum* sp. nov. Tabulation. Left, oblique dorsal view ; right, oblique ventral view. × c. 800.

DESCRIPTION. Theca ovoidal, an appearance of polygonality being imparted by the crests. The pericoel surface bears a coarse granulation, granules being rather regularly spaced. The crests are thin and high, with minute, inconspicuous perforations. Their distal edge is usually smooth, occasionally finely denticulate ; crests of a single individual may in part have smooth, in part denticulate, edges.

The apical prominence appears to be formed solely by the junction of crests bounding the four apical plates ; there appears to be no apical horn as such. Apical plate 1′ occupies the anterior extension of the sulcus ; since the sulcus is long and approaches the apex, plate 1′ is proportionately small. The six precingular plates are all quite large. Presence of an anterior intercalary plate was suspected but not confirmed ; if present, this plate is relatively small. Five well-developed postcingular plates are present ; plate 1‴ is reduced to accommodate a quadrate posterior intercalary plate. The antapex is occupied by a single, large plate.

The cingulum forms a strong laevorotatory spiral such that its two ends differ in antero-posterior position by roughly twice its width. There are six clear cingular plates, plus a seventh, diamond-shaped plate, here designated 7c, which lies between the posterior end of the cingulum and the sulcus. The sulcus is narrow and long, extending almost from apex to antapex.

An archaeopyle is not present in the holotype ; however, the paratype has a well-developed precingular archaeopyle formed by loss of plate 3″.

REMARKS. *Leptodinium alectrolophum* differs from all described species in its combination of crest and thecal morphology and tabulation. It resembles *Gonyaulacysta gongylos* in having a seventh polygonal plate at the posterior end of the cingulum, but differs in tabulation and crest form and shape. *Heslertonia heslertonense* has even higher crests ; the surface lacks similar granulation and the tabulation is again different.

In certain orientations, the high crests of this species produce a misleading resemblance to *Scriniodinium* : however, detailed study shows that no pericoel is present.

The form from the Aptian of Germany, figured by Eisenack (1958, pl. 22, fig. 4) as ?*Gonyaulax* sp., may well be attributable to this species.

Presence of only five postcingular plates presumably results from the trend of reduction of plate 1‴ ; thus plate 1‴ of *Leptodinium* corresponds to plate 2‴ of *Gonyaulacysta*.

OTHER SPECIES

The following species are retained in this genus and accord with the emended diagnosis :

Leptodinium arcuatum Klement 1960. Upper Jurassic (Upper Oxfordian); Germany.

Leptodinium maculatum Cookson & Eisenack 1961*b*. Eocene ; Rottnest Island, Western Australia.

Leptodinium membranigerum Gerlach 1961. Oligocene ; Germany.

Leptodinium mirabile Klement 1960. Upper Jurassic (?Oxfordian–Lower Kimmeridgian) ; Germany.

?*Leptodinium tenuicornutum* Cookson & Eisenack 1962*b*. Cretaceous (?Albian) ; Western Australia.

Genus *RAPHIDODINIUM* Deflandre 1936 : 184

TYPE SPECIES. *Raphidodinium fucatum* Deflandre 1936. Upper Cretaceous ; France.

REMARKS. This genus comprises highly condensed proximo-chorate cysts of ovoidal shape, characterized by possession of a very few extremely long spines, about 12 in number and up to twice the shell length. The shell surface bears low crests outlining a tabulation : the spines arise from crest nodes. The tabulation has not been determined, nor has an archaeopyle been reported ; the systematic position thus remains obscure. It is clearly a cyst genus, however, since spines arise from the cingulum.

Genus *PSALIGONYAULAX* nov.

DERIVATION OF NAME. Greek, *psalis*, low building with a vaulted roof ; a variant of the *Gonyaulax* tabulation type with terminal pericoels.

DIAGNOSIS. Bicavate dinoflagellate cysts, pericoel separated into two portions by broad median zone of contact with inner body. Outline spheroidal to ellipsoidal or subpolygonal with apical horn. Tabulation 3–4′, 1a, 6″, 6c, 6‴, 1p, 1⁗ determinable on periphragm, sutures in form of ridges of varied height and ornament. No spines arise from crest nodes. Surface of endophragm and periphragm smooth, granular, nodose, reticulate or punctate. Precingular archaeopyle formed by loss of plate 3″.

TYPE SPECIES. *Psaligonyaulax deflandrei* sp. nov. Upper Cretaceous (Cenomanian) ; England.

REMARKS. This new genus is distinguished from *Gonyaulacysta* by the presence of apical and antapical pericoels ; the species *Gonyaulacysta cassidata*, which has a closely similar tabulation pattern to that of the type species of *Psaligonyaulax* and which has an apical pericoel but no antapical pericoel, may well represent an intermediate form.

Psaligonyaulax is distinguished from *Scriniodinium* sensu stricto by the separation of the pericoel into two parts ; from the subgenus *Scriniodinium* by the presence of a clear tabulation ; from the subgenus *Endoscrinium* by possession of a posterior intercalary plate and an antapical plate.

Psaligonyaulax deflandrei sp. nov.

Pl. 14, figs. 7, 8 ; Text-fig. 35

1964. *Gonyaulax cassidata* Eisenack & Cookson ; Cookson & Hughes : 42, pl. 5, fig. 11 only.

DERIVATION OF NAME. Named in honour of Professor Georges Deflandre, who has published fundamental studies of dinoflagellates in the French Upper Cretaceous between 1932 and the present.

DIAGNOSIS. A *Psaligonyaulax* having a spindle-shaped outline, truncated posteriorly, with ovoidal inner body. Apical pericoel surmounted by bifid horn, antapical pericoel flattened. Tabulation 4′, 1a, 6″, 6c, 6‴, 1p, 1⁗. Crests of moderate height with smooth or denticulate edges. Cingulum broad, strongly spiral : sulcus narrower but widening posteriorly. Surfaces of endophragm and periphragm smooth or only minutely granular : an irregular scatter of tubercles may be present on periphragm.

HOLOTYPE. Geol. Surv. Colln. slide PF.3049(1). Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey, at 730 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype : overall length 75μ, breadth 44μ ; length of inner body 35μ, breadth 40μ. Range of dimensions : overall lengths 72 to 82μ, breadths 43 to 60μ.

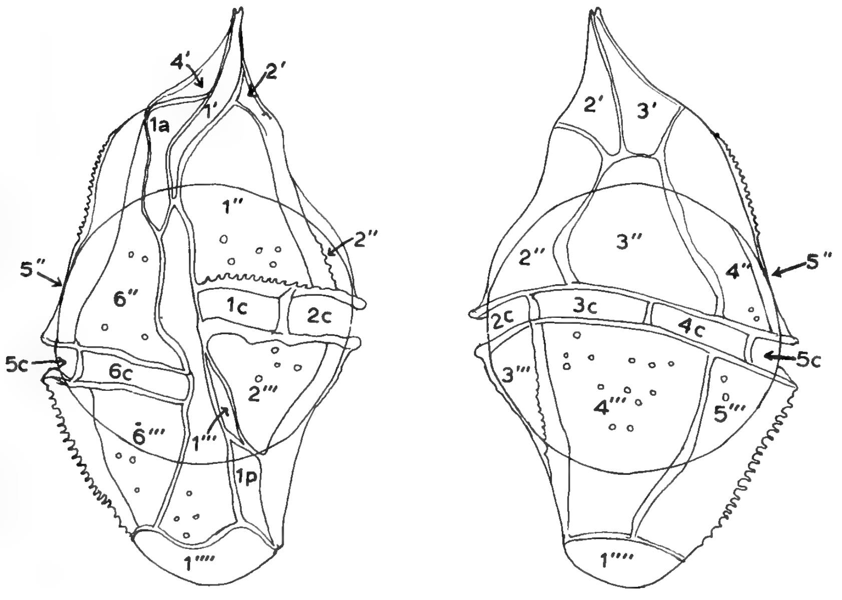


FIG. 35. *Psaligonyaulax deflandrei* sp. nov. Tabulation. Left, ventral view ; right, dorsal view (plate 3″ is missing). × c. 1000.

DESCRIPTION. The apical horn is more or less conical, a bifid appearance being imparted by the apical junction of crests separating the four apical plates. Plate 1′ is narrow and elongate, occupying the anterior prolongation of the sulcus ; the anterior intercalary plate is also rather elongate. Six precingular and six post-cingular plates are present : plate 1‴ is very reduced and elongate. A posterior intercalary plate separates plates 1‴ and 2‴ from the single plate occupying the antapex.

The cingulum forms a laevorotatory spiral such that its two ends differ in antero-posterior position by three times its width : six cingular plates are present. The sulcus is constricted in its median portion, but widens considerably as it approaches the antapex.

The crests are in part smooth, in part denticulate : they are sometimes very finely perforate. A scatter of tubercles may be present, their number and distribution varying considerably between individuals.

Plate 3″ is consistently lost in archaeopyle formation : its absence is not always obvious in unstained specimens, as a result of the delicacy and tranparency of the shell.

REMARKS. *Psaligonyaulax deflandrei* sp. nov. is present throughout the Cenomanian of the Fetcham Mill Borehole, but it is never abundant. Cookson & Hughes (1964) figured a representative of this species from the Cambridge Greensand (?Albian–Cenomanian) as *Gonyaulax cassidata*. The latter species, now *Gonyaulaesyta cassidata*, has a comparable distribution and a similar tabulation : it may be related to *P. deflandrei*, but intermediate forms are not known.

OTHER SPECIES

The species *Scriniodinium apaletum* Cookson & Eisenack 1960, from the Upper Jurassic of Australia and Papua, appears attributable to *Psaligonyaulax* : its tabulation has not, however, been described to date.

Following the reconsideration herein of the genera *Hystrichosphaeropsis* and *Rottnestia*, the species *R. simplicia* Cookson & Eisenack 1961*b*, which has poorly developed apical and antapical pericoels and lacks spines arising from crest nodes, becomes *Psaligonyaulax simplicia* (Tertiary ; Rottnest Island, Australia).

Genus *HYSTRICHOSPHAEROPSIS* Deflandre 1935

EMENDED DIAGNOSIS. Bicavate dinoflagellate cysts, pericoel divided by broad median zone of contact with inner body. Outline typically somewhat angular, apical and antapical periocoels typically quadrate in outline ; apical horn arising from former. Tabulation ?3–4′, ?1a, 6″, 6c, 6‴, 1p, 1⁗, determinable on periphragm ; sutures in form of ridges of varied height and ornamentation ; simple or furcate spines of varied length arising from some or all crest nodes. Surface of endophragm and periphragm smooth, granular, punctate, nodose or reticulate. Precingular archaeopyle formed by loss of plate 3″.

TYPE SPECIES. *Hystrichosphaeropsis ovum* Deflandre 1935. Upper Cretaceous ; France.

REMARKS. The name *Hystrichosphaeropsis* was originally proposed as a separate genus, but was later relegated to the status of a subgenus of *Hystrichosphaera* (Deflandre 1936*b*). Its status as a separate genus was implicitly revived by the inclusion of this name in a list of valid genera by Eisenack (1963*a* : 118).

The generic name *Rottnestia* was subsequently proposed by Cookson & Eisenack (1961b : 40–42). Deflandre, in a letter to the author (written in 1963 and here quoted by permission) comments as follows :

" Le genre *Rottnestia* Cookson et Eisenack 1961 est synonyme du genre *Hystrichosphaeropsis* Defl. 1935 (subgen. in Defl. 1937). Le type (*H. borussica* Eisenack) est tout à fait sembable à *H. ovum* Defl. 1935. Les autres espèces d'*Hystrichosphaeropsis* sont *H. simplicia* (C. et E.) et *H. wetzeli* ; Defl. 1935. "

On this basis, it appears necessary that the generic name *Rottnestia* should be abandoned. The revised diagnosis of *Hystrichosphaeropsis*, here formulated, incorporates in general the diagnostic features quoted in both earlier diagnoses (i.e. of *Hystrichosphaeropsis* and *Rottnestia*) ; but forms lacking nodal processes are excluded and attributed to the new genus *Psaligonyaulax*. The author was courteously permitted by Prof. Deflandre to examine the type species during a visit to Paris in 1961 ; the tabulation was elucidated to be as here quoted. The figures of *Rottnestia* suggest the same tabulation.

OTHER SPECIES

Although Prof. Deflandre considers *Rottnestia borussica* to be probably conspecific with *Hystrichosphaeropsis ovum*, this remains to be confirmed : the former species is thus provisionally retained as *Hystrichosphaeropsis borussica* (Tertiary ; Rottnest Island, Australia).

Hystrichophaeropsis wetzeli Deflandre 1935 (Upper Cretaceous ; France) accords with the revised diagnosis.

Genus ***CARPODINIUM*** Cookson & Eisenack 1962*b* : 489

TYPE SPECIES. *C. granulatum* Cookson & Eisenack 1962b. Lower Cretaceous (Aptian–Albian) ; Australia.

REMARKS. This genus was diagnosed in the following terms (1962*b* : 489) :

" Shell elongate—oval to ellipsoidal, divided almost equally by an equatorial girdle. Epitheca with a distinct horn, hypotheca devoid of horns or projections. Pre- and post-equatorial plates probably six in number, elongate trapezoidal and bordered with wings. The longitudinal furrow broadens gradually from the apex to the antapex. A pylome develops on the dorsal surface of the epitheca. "

In absence of full knowledge of the tabulation, the above diagnosis includes no characters, save possibly the posterior widening of the sulcus, which distinguish it from *Gonyaulax*, as accepted at the time of publication, or from *Gonyaulacysta* as defined by Deflandre and here redefined. The status of this genus must be regarded as questionable.

[Genus ***RHYNCHODINIOPSIS*** Deflandre 1935]

TYPE SPECIES. *Rhynchodiniopsis aptiana* Deflandre 1935. Lower Cretaceous (Aptian) ; France.

REMARKS. In his first full description of this genus (1936*a* : 32), Deflandre remarks on its apparent close relationship to *Gonyaulax*. Examination of his excellent figures suggests the tabulation 4–?5′, ?1a, 6″, 6g, 6‴, 1p, 1⁗ ; a precingular archaeopyle is present, formed by loss of plate 3″. Three distinguishing characteristics are cited by Deflandre—the presence of a strong, hollow, apical horn ; the presence of denticulate, aliform crests on sutures ; and the presence of strong curved spines arising from crest nodes along the edges of the cingulum. The first two characters are shared by many species of *Gonyaulacysta* ; the figures indeed strongly suggest a close affinity to *Gonyaulacysta jurassica*. The third distinguishing character does not alone warrant separation to generic level.

It is considered that this genus was, at the time of its publication, effectively a junior homonym of *Gonyaulax*, none of the characters cited warranting the creation of a new name. It is therefore proposed that the name *Rhynchodiniopsis* be abandoned and the single species, *R. aptiana*, from the Lower Cretaceous (Aptian) of France, be transferred to *Gonyaulacysta*.

Genus ***HYSTRICHODINIUM*** Deflandre 1935 : 229

EMENDED DIAGNOSIS. Proximo-chorate dinoflagellate cysts, spheroidal, ovoidal or polygonal in shape. Tabulation in general accord with *Gonyaulax* pattern, but not determined in detail. Long, hollow spines, rounded in cross-section and fairly stiff, arising from positions of plate boundaries : plate boundaries otherwise marked by low crests or not at all. Cingulum strongly or weakly helicoid, well-marked ; sulcus poorly marked. Length of spines variable, but typically exceeding ½ of shell width. Shell surface smooth, granular, punctate, nodose or areolate. A precingular archaeopyle formed, presumably by loss of plate 3″.

TYPE SPECIES. *Hystrichodinium pulchrum* Deflandre 1935. Upper Cretaceous ; France.

REMARKS. The generic diagnosis is emended to include reference to mode of archaeopyle formation and to specify the correspondence of spine position to sutures. This revision follows the examination of specimens of the type species preserved in flint (see below). The genus as now redefined differs from *Gonyaulacysta* in the height of sutural spines ; from *Xiphophoridium* in mode of archaeopyle formation ; and from *Heliodinium* in the rounded, not flattened, nature of the spines and the less well-marked sutures.

Hystrichodinium pulchrum Deflandre

Pl. 16, figs. 7, 8

1935. *Hystrichodinium pulchrum* Deflandre : 229, pl. 5, fig. 1 ; text-figs. 9–11.
1936*a*. *Hystrichodinium pulchrum* Deflandre ; Deflandre : 58, text-fig. 101.
1936*b*. *Hystrichodinium pulchrum* Deflandre ; Deflandre : 34, pl. 8, figs. 3–8, pl. 9, fig. 3.
1941. Dinoflagellate W. Wetzel, O. Wetzel & Deflandre, text-fig. 7.
1944. *Hystrichodinium pulchrum* Deflandre ; de Wit, unnumbered text-fig.
1952*a*. *Hystrichodinium pulchrum* Deflandre ; Deflandre, text-fig. 103.
1952*b*. *Hystrichodinium pulchrum* Deflandre ; Deflandre, text-fig. 300B.
1955. *Hystrichodinium pulchrum* Deflandre ; Valensi : 591, pl. 3, fig. 11.
1959. *Hystrichodinium pulchrum* Deflandre ; Gocht : 58, pl. 3, figs. 11*a*, *b*, pl. 5. fig. 7.
1961. *Hystrichodinium pulchrum* Deflandre ; Alberti : 14, pl. 8, figs. 6–10.
1963. *Hystrichodinium pulchrum* Deflandre ; Górka : 32, pl. 5, fig. 5.

MATERIAL (Figured). B.M.(N.H.) slide V.13937 (1, 2). Flint from the Chalk (no locality or horizon).

DIMENSIONS. Figured specimens : No. 1 : overall length 102μ, breadth 98μ, shell length 55μ, breadth 44μ. No. 2 : overall length 115μ, breadth 80μ ; shell length 55μ, breadth 35μ. Observed range ; overall lengths 102–115μ, breadths 80–101μ.

REMARKS. This species has long been known from the Upper Cretaceous flints, although its structure has not yet been fully determined. It appears to be synonymous with the species described by White (1842 : pl. 4 div. 3 fig. 6 ; 1844, pl. 8, fig. 5) and by Wilkinson (1846, pl. 8, figs. 2–3) as *Xanthidium spinosum* ; this species was subsequently transferred to *Hystrichosphaeridium* by Deflandre (1937*a* : 31) and to *Baltisphaeridium* by Downie & Sarjeant (1963 : 92) on taxonomic grounds, but has never been redescribed. Prolonged enquiry by the present author among the universities, libraries and museums of Britain indicates that the holotypes of White and Wilkinson are lost ; since *Hystrichodinium pulchrum* is well-defined and a name in widespread use, it is proposed that the earlier name *spinosum* be abandoned.

The above enquiry brought to light a number of unlocalized flint slides, in each case of unspecified source, which contain specimens of " xanthidia ", including a number of examples of *Hystrichodinium pulchrum*. Examination of these indicated the precingular character of the pylome and that the distribution of spines corresponds to the positions of sutures, necessitating revision of the generic diagnosis. A full restudy and redescription of this species, based on material extracted by chemical techniques, is clearly necessary.

OTHER SPECIES

The following species are here attributed to the genus *Hystrichodinium* and accord with the revised diagnosis :

Hystrichodinium compactum Alberti 1961. Lower Cretaceous (Valanginian) ; Germany.

Hystrichodinium furcatum Alberti 1961. Lower Cretaceous (Hauterivian) ; Germany.

Hystrichodinium oligacanthum Deflandre & Cookson 1955. Lower Cretaceous ; Australia.

Hystrichodinium ramoides Alberti 1961. Lower Cretaceous (Barremian) ; Germany.

The two remaining species previously attributed to this genus are considered only doubtfully referable to the revised genus. ?*Hystrichodinium amphiacanthum* Cookson & Eisenack 1958, has appendages which are polar in position and may warrant erection as a new genus. ?*H. parvum* Alberti 1961, from the Lower Cretaceous (Aptian) of Germany, remains of uncertain generic allocation and merits a full restudy.

Genus ***HELIODINIUM*** Alberti 1961 : 33

EMENDED DIAGNOSIS. Proximo-chorate dinoflagellate cysts, spheroidal, ovoidal or subpolygonal in shape, with tabulation ?3′, ?0a, 6″, ?0c, 6‴, ?0p, 1⁗. Sutures faintly marked by ridges or low crests, from which arise flattened, dagger to ribbon-like, very flexible processes ; processes typically simple, bifurcate or multi-furcate. Cingulum strongly or weakly helicoid, bounded by low crests : sulcus less well marked. Shell surface smooth, granular or punctate. Precingular archaeopyle formed by loss of plate 3″.

TYPE SPECIES. *Heliodinium voigti* Alberti 1961. Lower Cretaceous (Barremian) ; Germany.

REMARKS. The generic diagnosis is emended to incorporate fuller reference to the tabulation and to include reference to the mode of archaeopyle formation. *Heliodinium* is distinguished from *Hystrichodinium* on the character of its processes.

Heliodinium voigti Alberti

Pl. 16, fig. 2 ; Text-fig. 36

1961. *Heliodinium voigti* Alberti : 33, pl. 8, figs. 1–5.

EMENDED DIAGNOSIS. A *Heliodinium* having a subpolygonal shell, epitract almost conical and hypotract in form of truncated cone. Tabulation ?3′, ?0a, 6″, ?0c, 6‴, ?0p, 1⁗ ; sutures generally marked only by low ridges, but cingulum and antapex bordered by low crests. Processes dagger-like, frequently highly folded, length less than half shell length ; distal ends of processes typically simple, rarely bifurcate or trifurcate. Shell surface smooth or only minutely granular.

HOLOTYPE. Preparation No. A26, Geologisches Institut der Universität, Tübingen, Germany. Lower Cretaceous (Upper Barremian) ; Haverlahwiese, Germany.

MATERIAL (figured). Geol. Surv. Colln. slide PF.3035(4). Chalk, H. M. Geological Survey Borehole, Fetcham Mill, Surrey, at 840 feet depth. Upper Cretaceous (basal Cenomanian).

DIMENSIONS. Holotype : shell length 48μ, breadth 38μ, length of processes 16–22μ. Range of German specimens : shell length 48–60μ, breadth 38–56μ, length of processes 16–36μ. Specimen here figured : overall length c.125μ, breadth c.105μ : shell length 62μ, breadth 45μ.

DESCRIPTION. This species occurs in low numbers in the assemblages from the Chalk at 840 and 810 feet depth (basal Cenomanian) in the Fetcham Mill bore. Although a number of specimens were available for study, the majority proved unsuitable as a result of distortion or unfortunate orientation : the figured specimen was the only one capable of full study. It was thus not possible to confirm details of the apical structure.

Plate 1′ is elongate and corresponds to the apical prolongation of the sulcus. At least two other apical plates appear to be present : no anterior intercalary plate could be distinguished. Six precingular and six postcingular plates are present ; no posterior intercalary plate was distinguished. The antapex is occupied by a single plate.

The cingulum forms a strong laevorotatory spiral whose two ends differ in antero-posterior position by three times its width. There appears to be no separation into cingular plates. The sulcus is narrow and extends to the antapex.

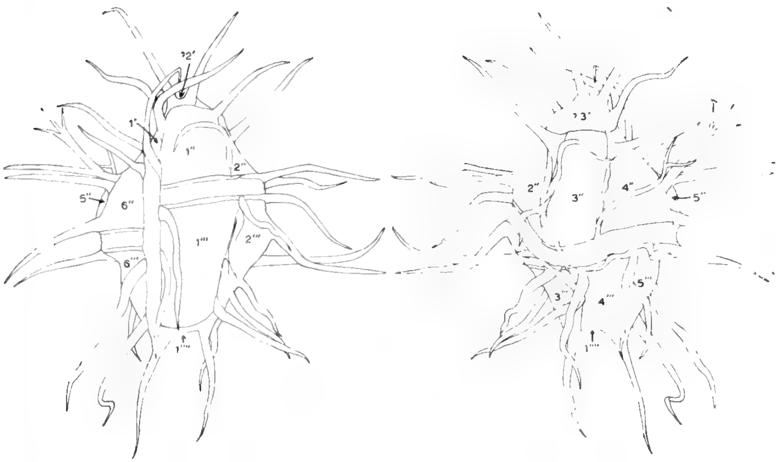


FIG. 36. *Heliodinium voigti* Alberti. Tabulation. Left, ventral view ; right, dorsal view (plate 3″ is missing). × c. 500.

The shell surface appears devoid of ornamentation. The processes are flattened and very flexible, generally simple—one process in the figured specimen is bifurcate, one trifurcate.

Plate 3″ is generally lost in pylome formation.

REMARKS. The diagnosis of this species is emended to incorporate new observations. Alberti (1961 : 33) noted the presence of an archaeopyle in one specimen, but did not refer to this in the diagnosis.

The stratigraphic range of the German specimens is Lower Barremian to ?Lower Aptian : the English occurrence thus represents a vertical extension of this range.

Heliodinium patriciae Neale & Sarjeant

Pl. 16, fig. 1

1961. *Heliodinium patriciae* Neale & Sarjeant : 451, pl. 19, fig. 3 ; text-fig. 7.

REMARKS. Re-examination of the holotype (B.M.(N.H.) slide V.51710), and other specimens, suggests a similar tabulation to that of *H. voigti* ; the mode of archaeopyle formation was not determined. In the original text fig. 7, the number of processes shown arising from the cingulum margins is now considered to be somewhat exaggerated ; the figure is correct in all other particulars.

B. Genera with apical archaeopyle

Genus ***MEIOUROGONYAULAX*** nov.

DERIVATION OF NAME. Greek, *meiouros*, curtailed, shortened ; a variant of the *Gonyaulax* tabulation type shortened by loss of the apex in archaeopyle formation.

DIAGNOSIS. Proximate dinoflagellate cysts, spherical, ellipsoidal, ovoidal or polyhedral, with the tabulation, 4′, 0–1a, 6″, 6g, 5–6‴, 0–1p, 0–1 p.v., 1⁗. Cingulum strongly or weakly helicoid ; sulcus generally or constantly extending on to epitract. Sutures in form of low ridges or bearing crests of varied form (smooth, denticulate or spinous ; perforate or imperforate). Height of crests always less than $\frac{1}{4}$ of shell width. Surface smooth, granular, nodose, punctate or reticulate. Archaeopyle formed by loss of apical plates, part of plate 1′ sometimes left attached to shell ; not all individuals show an archaeopyle.

TYPE SPECIES. *Meiourogonyaulax valensii* sp. nov., Middle Jurassic.

REMARKS. This genus presently contains a small group of Jurassic species ; unpublished data available to the author suggests the probability that a number of additional species will be described in the future from the Lower and Middle Jurassic.

The apex has in no case been satisfactorily seen in position. The number of apical plates is deduced from the irregular profile of the archaeopyle and may be subject to future correction.

Meiourogonyaulax valensii sp. nov.

Pl. 15, fig. 7 ; Text-fig. 37

1953. *Gonyaulax* sp. indet., Valensi : 27, pl. 2, figs. 12, 13.

DERIVATION OF NAME. Named after Lionel Valensi, who published the first full descriptions of Middle Jurassic dinoflagellate/acritarch assemblages.

DIAGNOSIS. A *Meiourogonyaulax* having a broadly ellipsoidal theca ; lacking apex in all specimens seen. Tabulation ?4', 0a, 6", 6c, 6''', 1p, 1 p.v., 1''''. Crests of moderate height, slightly striated and irregularly perforate, with smooth or finely denticulate distal edges. Spines present at some crest nodes. Cingulum strongly spiral, relatively broad ; sulcus broadening posteriorly, subdivided by low ridges. Shell surface punctate or alveolar.

HOLOTYPE. Specimen B.S.60 (L. Valensi preparation), Laboratoire de Micropaléontologie, École Pratique des Hautes Études, Paris. Chert from Airvault, Poitou, France. Middle Jurassic (Bathonian).

DIMENSIONS. Holotype : overall length 70μ, breadth 70μ ; shell length, approx. 60μ, breadth approx. 50μ ; width of transverse furrow c.6μ.

DESCRIPTION. Although this species is based on Valensi's single specimen, the author has also seen a number of specimens in material from the Bathonian of the Aquitaine Basin, unfortunately not available for description.

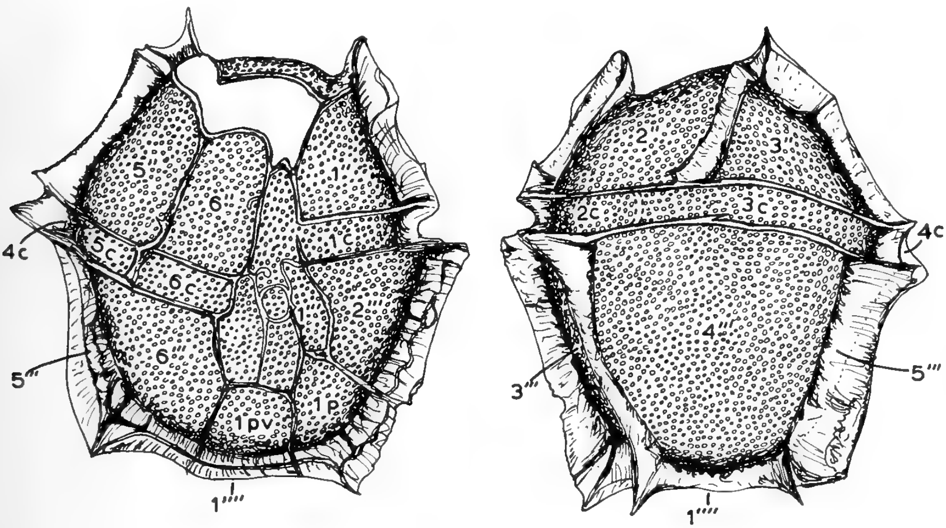


FIG. 37. *Meiourogonyaulax valensii* sp. nov. Tabulation. Left, ventral view ; right, dorsal view. × c. 1000.

From the angular profile of the apical archaeopyle, the former presence of at least four apical plates is deduced. There is no anterior intercalary plate. Six precingular plates are present, plate 6″ being slightly reduced. Six postcingular plates are present, plate 1‴ being reduced and elongate, separated from the antapex by a moderately large posterior intercalary plate. The antapex is occupied by a single large plate and is separated from the sulcus by a quadrate posterior ventral plate.

The cingulum forms a strong laevorotatory spiral such that its two ends differ in antero-posterior position by over twice its width. It is clearly subdivided into six cingular plates. The sulcus is roughly wedge-shaped, broadening towards the posterior ; it bears low ridges forming an irregular pattern.

The shell surface is alveolar to punctate. The crests are moderately high, faintly striate and intermittently perforated ; their distal edges are in part smooth, in part finely denticulate. Crest nodes are strengthened by stout spines in some or all cases. The crests bordering the sulcus are very reduced.

REMARKS. Professor Georges Deflandre permitted the author and Mr. R. J. Davey to examine the holotype during visits to Paris, and also provided the photograph ; his courtesy is gratefully acknowledged.

Meiourogonyaulax valensii sp. nov. is distinguished from the other species of this genus in the detail of tabulation and the nature of the crests.

OTHER SPECIES

The following species are here attributed to *Meiourogonyaulax* gen. nov. and accord with the diagnosis of this genus :

Meiourogonyaulax bulloidea (Cookson & Eisenack 1960*b*). Upper Jurassic (?Tithonian) ; Western Australia.

Meiourogonyaulax cristulata (Sarjeant 1959). Middle Jurassic (Callovian) ; England.

A third species is doubtfully attributed to the genus :

?*Meiourogonyaulax caytonensis* (Sarjeant 1959). Middle Jurassic (Callovian) ; England.

The mode of archaeopyle formation in this latter species is not clear. The holotype has an intact apex, but lacks plate 2″, suggesting a precingular archaeopyle in a unique position : other specimens lack an apex. Assignment to *Meiourogonyaulax* is thus provisional.

Genus ***XIPHOPHORIDIUM*** nov.

DERIVATION OF NAME. Greek, *xiphos*, sword : *phor-*, suffix meaning to bear, carry.

DIAGNOSIS. Proximo-chorate dinoflagellate cysts, spheroidal to ovoidal or polygonal withtabulation ?4′, 1a, 6″, 0–1p, 6‴, 1⁗. Cingulum strongly or weakly

spiral, laevo-rotatory. Apical and antapical horns lacking. Sutures marked by high crests bearing long, dagger-like spines, broadly spaced ; crests bordering cingulum especially high and prominent. Surface smooth, granular, punctate or tuberculate. Archaeopyle formed by loss of apical plates ; not all individuals have an archaeopyle.

TYPE SPECIES. *Hystrichodinium alatum* Cookson & Eisenack 1962*b*. Cretaceous (?Upper Aptian–Cenomanian) ; Western Australia.

REMARKS. This genus comprises forms with high, pronouncedly spinose crests. It is distinguishable from *Heliodinium*, *Hystrichodinium* and *Ctenidodinium* by the mode of archaeopyle formation, from *Heliodinium* and *Hystrichodinium* also by the fact that the sutural spines arise from crests ; and from *Ctenidodinium* also by the fact that the cingulum is bordered on *both* sides by high crests.

Xiphoridium alatum (Cookson & Eisenack)

Pl. 16, fig. 11

1962*b*. *Hystrichodinium alatum* Cookson & Eisenack : 478, pl. 2, figs. 1–4.

EMENDED DIAGNOSIS. A *Xiphophoridium* having an ovoidal to nearly globular shell, shell wall thin. Tabulation ?4′, 1a, 6″, 6‴, ?0p, 1⁗ ; plates bounded by very high crests bearing long, dagger-like spines, crest curving inwards between bases of spines. Cingulum weakly spiral, of moderate breadth and bordered by especially high crests ; sulcus also of moderate breadth, extending to antapex. Shell surface not, or only minutely, granular, bearing numerous tubercles, sometimes apparently arranged to plate margins, generally without obvious arrangement. Apical archaeopyle present.

HOLOTYPE. Specimen no. P.21272, National Museum, Victoria, Australia.

MATERIAL (figured). Geol. Surv. Colln. slide PF.3051(1). Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey, at 840 feet depth. Upper Cretaceous (basal Cenomanian).

DIMENSIONS. Holotype : overall length 125μ, breadth 96μ : length of shell 70μ, breadth 52μ. Range of Australian specimens : overall lengths 100–102μ, overall breadths 92–100μ. As a result of orientation or preservation, it did not prove possible to obtain detailed measurements of the English specimens, but dimensions appear comparable.

DESCRIPTION. This species occurs infrequently throughout the English Cenomanian, some 20 specimens having been encountered. The specimen figured, seen in terminal view, was the best-preserved and allowed determination of the tabulation: all other specimens were damaged or distorted to some extent. It was not possible to prepare a satisfactory figure.

The shape of the archaeopyle is that of a ragged polygon with a narrow sulcal notch, suggesting that four apical plates were originally present. Six precingular plates are present, plate 6″ being reduced to accommodate a quadrate anterior intercalary plate. Six postcingular plates are present ; no posterior intercalary plate could be distinguished in the specimens studied. The antapex is occupied by a single polygonal plate.

The cingulum is weakly spiral, laevorotatory ; its structure was not clear in the English specimens, but the photographs of the Australian specimens suggest a division into cingular plates (?6).

The crests are delicate, not or only minutely perforate : the spines arise simply as outgrowths of the crests and are somewhat flattened and dagger-like. The shell wall appears to lack ornament other than the tubercles.

REMARKS. In their original description of this species, Cookson & Eisenack noted the clear presence of tabulation and recognized this as a separating character from other species of *Hystrichodinium*, in which they then placed it. They do not record the presence of an apical archaeopyle but this feature is suggested in one of their figures (pl. 2, fig. 2). The diagnosis is here emended to include reference to the tabulation and the possession of an apical archaeopyle.

Genus ***BELODINIUM*** Cookson & Eisenack 1960*b* : 249

TYPE SPECIES. *Belodinium dysculum* Cookson & Eisenack 1960*b*. Upper Jurassic (Tithonian) ; Australia.

REMARKS. This genus was diagnosed in the following terms :

> " Shell elongate, unequally divided by a circular girdle. Main body marked into fields by delicate ledges : epitheca with a hollow membraneous horn, hypotheca with a flattened membraneous expansion."

In the absence of a full knowledge of the tabulation, distinction of this genus depends on the circular nature of the cingulum and the presence of an antapical pericoel. The description of the type species (Cookson & Eisenack 1960*b* : 250) makes it clear that archaeopyle formation is by loss of the apical plates. The authors state that their interpretation of the genus is " provisional " and " incomplete " : a fuller study of the genus and a revision of the diagnosis are clearly necessary before its status can be validly assessed.

Genus ***MICRODINIUM*** Cookson & Eisenack 1960*a* : 6

EMENDED DIAGNOSIS. Proximate dinoflagellate cysts, spheroidal to ovoidal in shape and usually small. Epitract smaller than hypotract. Tabulation 1′, 0–?1a, 6″, 6c, 6‴, 1p, 1⁗, with differentiation in some species of additional plates in ventra, region. Cingulum broad, weakly spiral ; sulcus broad, extending from apex to antapex. Sutures bearing crests in form of low ridges (perforate or imperforate),

smooth, denticulate, or bearing spines of varying lengths ; alternatively sutures marked by lines of closely set spines. Shell surface smooth, granular, punctate or tuberculate. Archaeopyle formation by loss of single apical plate.

TYPE SPECIES. *Microdinium ornatum* Cookson & Eisenack 1960*a*. ?U. Aptian–Turonian : Australia.

REMARKS. At the time when it was proposed, this genus was technically invalid, since its tabulation falls within the limits specified for *Gonyaulax*. However, *Microdinium* is now recognized to be a cyst genus and, regarded as such, becomes a valid entity, since its tabulation does not accord with that of *Gonyaulacysta* either in the original definition of Deflandre or as here emended.

Representatives of this genus are relatively frequent in the English Cenomanian. The generic diagnosis is emended to accommodate variations in morphology exhibited by these forms.

Microdinium differs from the majority of fossil dinoflagellate cysts in having an apical archaeopyle ; from *Meiourogonyaulax* and *Xiphophoridium* in having only a single apical plate ; and from *Glyphanodinium* in having six precingular plates.

***Microdinium* cf. *ornatum* Cookson & Eisenack**

Pl. 16, figs. 3–6 ; Text-fig. 38

1960*a*. *Microdinium ornatum* Cookson & Eisenack : 6, pl. 2, figs. 3–8, text-figs. 2–4.

MATERIAL (Figured). Geol. Surv. Colln. slide PF.3050(1). Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey, at 670 feet depth. Upper Cretaceous (Upper Cenomanian).

DIMENSIONS. Figured specimen : length 40μ, breadth 32μ. Range length c.30–45μ, breadth c.22–35μ.

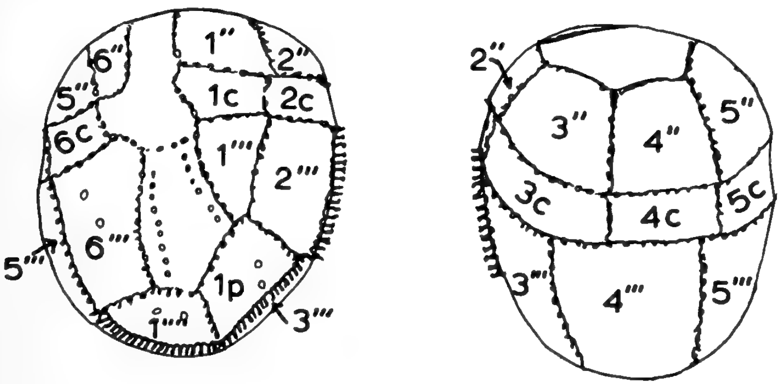


FIG. 38. *Microdinium* cf. *ornatum* Cookson & Eisenack. Tabulation. Left, ventral view ; right, dorsal view (the apex is missing). × c. 1250.

DESCRIPTION. This form occurred in moderate abundance in the upper levels of the Cenomanian of the Fetcham Mill Borehole, over 20 specimens having been seen ; the apex was missing in all specimens seen.

The shell is ovoidal in shape, with a somewhat flattened antapex and an apex truncated by the archaeopyle. Six precingular and six postcingular plates are present. The presence of an anterior intercalary plate was suggested in some specimens, but could not be confirmed as a result of distortion around the archaeopyle. Plates 1''' and 2''' are reduced to accommodate a large posterior intercalary plate ; this is of comparable size to the single antapical plate, some specimens indeed give the impression of having two antapical plates.

The cingulum is very broad and not hollowed ; it is weakly spiral, laevorotatory, its two ends scarcely differing in antero- posterior position. The sulcus is broad throughout its length, but broadest as it approaches the antapex : ventral plates are absent.

The shell surface is generally quite smooth, but bears a scatter of tubercles, some of which are aligned parallel to sutures ; the number and arrangement of tubercles varies between individuals. The sutures bear closely set spines, capitate and of constant length, giving almost the impression of perforate crests : in vertical view, these give the impression of a string of beads.

REMARKS. These English Cenomanian forms generally closely resemble *Microdinium ornatum* as described from Australia, but differ in two details—the absence of a plate separating the posterior end of the cingulum from the sulcus, and the form of the crests, which are constantly in the form of closely set spines. It is highly probable that they fall within the range of variation of *M. ornatum,* since they accord closely with the photographs and since Cookson & Eisenack state (p. 7) that " the

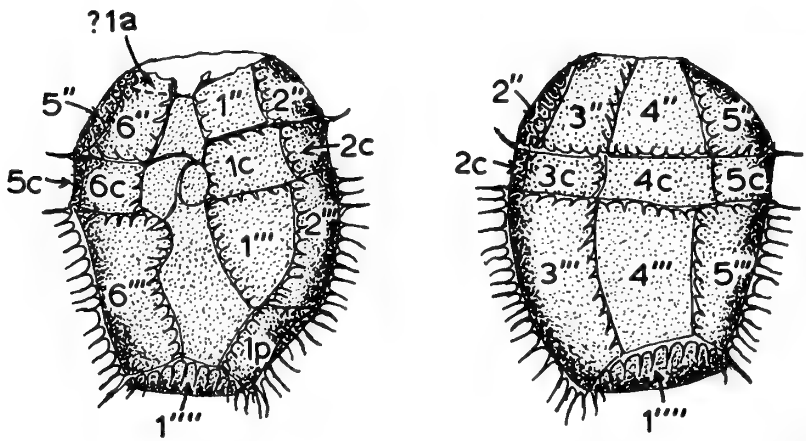


FIG. 39. *Microdinium setosum* sp. nov. Tabulation. Left, ventral view ; right, dorsal view. × c. 1250.

outer edge of the ledges may be missing " in some specimens ; it is also possible that representatives of two species have been placed together by those authors. For the present, it is considered appropriate that the English forms should be compared with, and not placed within, the species *M. ornatum*.

Microdinium setosum sp. nov.

Pl. 16, figs. 9, 10 ; Text-fig. 39

DERIVATION OF NAME. Latin, *setosus*, bristly ; referring to the spines on the sutures.

DIAGNOSIS. A *Microdinium* having an ovoidal shell with somewhat flattened antapex. The epitract considerably smaller than the hypotract ; a broad cingulum, weakly spiral, divides them. Tabulation ?1', 0a, 6'', 6c, 6''', 1p, 1'''' : two additional plates present in ventral region between two ends of cingulum. Sutures bearing low crests from which arise spines of moderate length, simple and well spaced ; shell surface minutely but densely granular. Apex characteristically lost in the pylome formation.

HOLOTYPE. Geol. Surv. Colln. slide PF.3046(2). Chalk, H.M. Geological Survey Borehole, Fetcham Park, Surrey, at 840 feet depth. Upper Cretaceous (basal Cenomanian).

DIMENSIONS. Holotype : overall length 35μ, breadth 30μ ; shell length 33μ, breadth 24μ. Range of dimensions : overall lengths 33 to 38μ, breadths 24 to 37μ.

DESCRIPTION. This species is moderately abundant in the lower levels of the Cenomanian of the Fetcham Mill Borehole, over 30 specimens having been seen. The apex is presumed to have consisted of a single plate, but it was lost in the majority of specimens seen. In a few, the archaeopyle " lid " was still attached, but too buckled for its character to be determined.

Six precingular and six postcingular plates are present, the former being consistently smaller than the latter in the proportion that the epitract is smaller than the hypotract. Plates 1''' and 2''' are reduced : a posterior intercalary plate separates plate 2''' from the antapex. As in *M.* cf. *ornatum*, plate 1p and the antapical plate are of comparable size and in some specimens look more like paired antapical plates.

The cingulum is broad, not hollowed, and very weakly spiral, its two ends scarcely differing in antero-posterior position. It is divided into six cingular plates ; two ventral plates lie between its two ends and divide the sulcus into an epitractal and a hypotractal portion.

The crests are low and bear simple, flexuous spines, the crest margin being scalloped between spine bases. The surface bears a uniform, dense cover of minute granules.

REMARKS. *Microdinium setosum* sp. nov. differs from *M. ornatum* in crest character, detail of tabulation, and granular surface. It is placed in *Microdinium* on the basis of general structure and apical archaeopyle : possession of only one apical plate was presumed but not confirmed.

Genus *GLYPHANODINIUM* Drugg 1964

TYPE SPECIES. *Glyphanodinium facetum* Drugg 1964. Palaeocene (Danian) ; California, U.S.A.

REMARKS. This is a genus of distinctive proximate dinoflagellate cysts of pentagonal shape, with the tabulation ?1′, 0a, 6c, 6‴, 1p, 1 p.v., 1⁗, the archaeopyle being formed by loss of the single (?) apical plate. The cingulum is situated high on the test, the epitract being thus small, the hypotract large. The overall shell size is small. It differs from *Meiourogonyaulax* in the apparent number of apical plates, and from *Microdinium* in overall shape and the presence of only five precingular plates.

Genus *EISENACKIA* Deflandre & Cookson 1955 : 258

1954. *Eisenackia* Deflandre & Cookson : 1236 (name only).

EMENDED DIAGNOSIS. Proximate dinoflagellate cysts, spheroidal or ovoidal in shape, with the tabulation 2–3′, 6″, ?6c, 6‴, 2p, 1⁗ ; additional plates occupy ventral area, there being no sulcus as such. Plates consisting of raised areas of shell surface, isolated from one another by pattern of " channels " corresponding in position to sutures. (It is here proposed that such inverse equivalents of sutures be termed " fossae ".) Cingulum weakly helicoid. Shell surface typically reticulate, possibly also granular or punctate. Apical archaeopyle formed by loss of apical plates.

TYPE SPECIES. *Eisenackia crassitabulata* Deflandre & Cookson 1955. Paleocene to Lower Eocene ; Australia.

REMARKS. The diagnosis is emended to stress the characteristic form of the tabulation, as plates separated by fossae, and to include reference to the mode of archaeopyle formation. The latter character was remarked on by Deflandre & Cookson (1955 : 260) in the description of the type species.

C. Genera with epitractal archaeopyle

Genus *RHAETOGONYAULAX* nov.

DERIVATION OF NAME. Refers to the occurrence of the type species in the Rhaetian (Rhaetic) Stage, uppermost Triassic, and to possession of a *Gonyaulax* type of tabulation.

DIAGNOSIS. Proximate dinoflagellate cysts, spindle-shaped or biconical, typically with the tabulation 4′, 1a, 6″, 6‴, 1p, 1⁗ : tabulation well or poorly marked by ridges or partially or entirely indeterminable. Cingulum strongly or weakly spiral, laevorotatory, divided into plates (?6c) or without such division. Surface smooth, granular, nodose, punctate or reticulate ; ornamentation may mask the tabulation. Archaeopyle (where present) epitractal, formed by schism of shell immediately anterior to cingulum.

TYPE SPECIES. *Gonyaulax rhaetica* Sarjeant, 1963a. Upper Triassic (Rhaetic) ; England.

REMARKS. This genus is created to accommodate the earliest known species having a tabulation of *Gonyaulax* type. The shape is unlike that of any other known fossil species having such a tabulation ; the plate boundaries are so poorly marked as to make it seem probable that any descendants would be non-tabulate. For these reasons, it is considered that a relationship with the species attributed to the genus *Dichadogonyaulax* gen. nov. is unlikely. Later genera having a spindle-shaped outline (*Kalyptea* ; *Netrelytron*) appear to consistently form precingular archaeopyles.

OTHER SPECIES

The following species also accords with the diagnosis of this genus and is here included in *Rhaetogonyaulax* accordingly : *Rhaetogonyaulax chaloneri* (Sarjeant 1963*a*). Upper Triassic (Rhaetic) ; England.

Genus ***DICHADOGONYAULAX*** nov.

DERIVATION OF NAME. Greek, *dichados*, half : refers to the almost median schism of the shell, so that typically half shells are encountered, and to the *Gonyaulax* —type tabulation.

DIAGNOSIS. Proximate dinoflagellate cysts, spheroidal, ovoidal, ellipsoidal or polyhedral, having the tabulation 3–5′, 0–?1a, 6″, 5 6‴, 1p, 1⁗ : sulcus divided into plates or undivided, ventral region may show division into additional small plates. Cingulum strongly or weakly spiral, laevorotatory. Apical horn may be present ; median and antapical horns lacking. Sutures in form of low ridges bearing crests of varied form (smooth, denticulate or spinous ; perforate or imperforate) ; or marked by lines of spines. Archaeopyle (where present) epitractal, by schism of shell immediately anterior to cingulum.

TYPE SPECIES. *Gonyaulax culmula* Norris 1965. Upper Jurassic (Portlandian) ; England.

REMARKS. Norris (1965) has described a group of species from the Portlandian which have in common their general morphology and mode of archaeopyle formation, but whose tabulation accords sometimes to the *Gonyaulax* pattern, sometimes to that of *Leptodinium*. The tabulation of the type species, which lacks an anterior intercalary plate but possesses six postcingular plates, is indeed intermediate in character. On this basis, it is considered that common characters outweigh the small tabulation differences and that the diagnosis should embrace all forms with epitractal archaeopyles and generally similar morphology.

OTHER SPECIES

The following species also accord with the diagnosis of this genus :

Dichadogonyaulax pannea (Norris 1965) comb. nov. Upper Jurassic (Upper Kimmeridgian–Portlandian) ; England.

D. schizoblata (Norris 1965) comb. nov. Upper Jurassic (Upper Portlandian) ; England.

D. Genera with cingular archaeopyle

Genus *CTENIDODINIUM* Deflandre 1938 : 181

EMENDED DIAGNOSIS. Proximo-chorate dinoflagellate cysts, spheroidal, ovoidal, ellipsoidal or polygonal, having the tabulation 3–4′, 0–1a, 6″, 6c, 6‴, 1p, 0–1 p.v., 1⁗ ; sutures in form of low ridges bearing crests of varied form, typically but not constantly high and denticulate. Cingulum strongly or weakly spiral, laevo-rotatory ; suture on anterior margin of cingulum lacking crest, crest on posterior margin very high. Archaeopyle (where present) formed by schism along cingulum.

TYPE SPECIES. *Lithodinia jurassica* var. *ornata* Eisenack 1935. Middle Jurassic (Callovian) ; Germany.

REMARKS. The diagnosis is emended to include reference to tabulation and mode of archaeopyle formation ; the latter, in combination with the unequal crest development on either side of the cingulum, characterizes the genus. Both species currently attributable to the genus occur in the Middle to Upper Jurassic (Callovian to Oxfordian), the type species being known to range up into the Lower Oxfordian.

OTHER SPECIES

The following species also accords with the revised diagnosis of the genus :

Ctenidodinium tenellum Deflandre 1938. Upper Jurassic (Oxfordian) ; France.

Genus *WANAEA* Cookson & Eisenack 1958 : 57

TYPE SPECIES. *Wanaea spectabilis* Cookson & Eisenack 1958. Upper Jurassic ; New Guinea.

REMARKS. W. R. Evitt, in litt., has informed the writer that this genus comprises detached epitracts and hypotracts of a genus with a *Gonyaulax*-pattern tabulation. High crests, perforated in varying degree to give a fringe-like appearance, border the cingulum : crests elsewhere on the shell are marked only by low ridges. Archaeopyle formation apparently results from schism along the cingulum, but the mechanism of the process appears more complicated than in *Ctenidodinium*. A full study of the genus is understood to be in press.

E. Genera with archaeopyles formed by other means

Genus *PLURIARVALIUM* Sarjeant 1962*a* : 260

TYPE SPECIES. *Pluriarvalium osmingtonense* Sarjeant 1962*a*. Upper Jurassic (Upper Oxfordian) ; England.

Pluriarvalium osmingtonense Sarjeant

Text-fig. 40

1962*a*. *Pluriarvalium osmingtonense* Sarjeant : 262, pl. 1, fig. 5 ; text-fig. 6.

REMARKS. This species is relatively abundant in certain horizons of the Upper Jurassic ; all specimens observed to date are either intact or severely damaged and

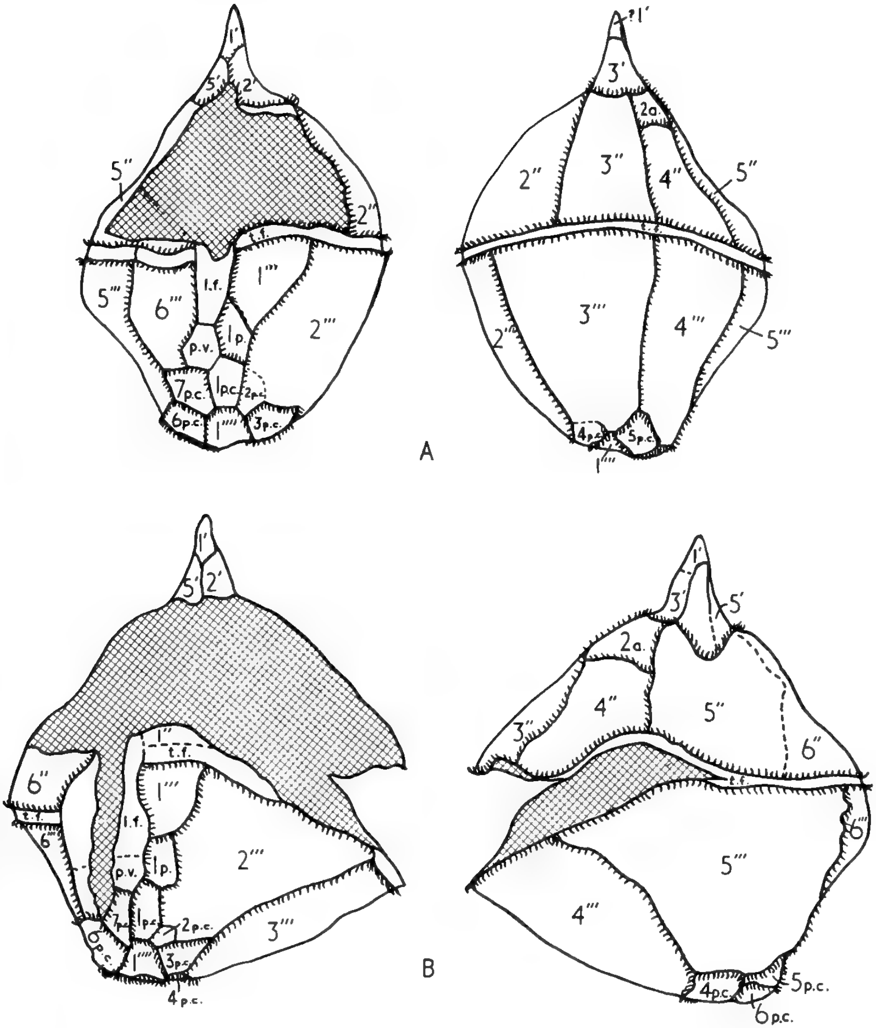


FIG. 40. *Pluriarvalium osmingtonense* Sarjeant. Two damaged specimens, showing how the anterior portion of the ventral surface is apparently lost in archaeopyle formation. Left, ventral view ; right, dorsal view. × c. 500.

crumpled. Study of the damaged specimens suggests that archaeopyle formation may occur by loss of the anterior ventral surface (see Text-fig. 40): such a method has not been observed in any other known dinoflagellate cyst. Further studies are needed before this suggestion can be confirmed; but certainly, no specimens yet observed give suggestion of archaeopyle formation by more familiar methods.

The holotype and paratypes of this species are in the collections of the Micropalaeontology Laboratory, Department of Geology, University of Sheffield.

CONCLUSIONS

The characteristics and known stratigraphic distribution of the twenty-one valid genera here considered are summarized in the accompanying Table. At present, no coherent picture emerges regarding the stratigraphical distribution of the different archaeopyle types: fuller studies of critical intermediate assemblages are clearly necessary. All four principal modes of archaeopyle formation were operative by the Upper Jurassic and it seems likely that these represent four divergent lines of evolution. *Rhaetogonyaulax* may represent a trend towards non-tabulate cysts of spindle-shape; *Acanthogonyaulax* towards non-tabulate, densely spinose forms; and the ancestors of *Hystrichosphaera* may well be found in species of *Gonyaulacysta* with progressively lower crests bearing progressively higher spines.

Dinoflagellate cysts basically having a *Gonyaulax*-type tabulation are shown to be dominant elements in Upper Jurassic and Lower Cretaceous assemblages, declining in importance (*Hystrichosphaera* excepted) in the Upper Cretaceous; rare in the lowest Tertiary; and apparently not represented after the Eocene. Their stratigraphic importance is thus greatest in the Upper Jurassic and Lower Cretaceous, where rapid evolution and limited vertical range combine to render many species satisfactory zonal indices.

TABLE 4

GENUS	TABULATION: Apical plates	Intercalary	Precingular Plates	Cingular Plates	Postcingular Plates	Posterior Intercalary Plates	Antapical Plates	Additional Plates (if present)	FORM OF SUTURES	TYPE OF ARCHAEOPYLE	OTHER SPECIAL FEATURES	OVERALL SHELL FORM	KNOWN STRATIGRAPHIC RANGE
Rhaetogonyaulax	4	1	6	6	6	1	1	—	LOW RIDGES OR INDETERMINABLE	EPITRACTAL	SPINDLE SHAPED SHELL	PROXIMATE	U Triassic (Rhaetian)
Gonyaulacysta	3 – 4	0 – 1	6	6	6	1	1	0 – 1 p v Ventral plates sometimes present	CRESTS OR LINES OF SPINES (HEIGHT LESS THAN 1/4 SHELL DIAMETER)	PRECINGULAR	APICAL HORN OFTEN PRESENT	PROXIMATE	M Jurassic (Bajocian) to U Cretaceous (Senonian)
Meiourogonyaulax	4	0 – 1	6	6	5 – 6	0 – 1		0 – 1 p v	LOW RIDGES OR CRESTS	APICAL	—	PROXIMATE	M – U Jurassic (Bathonian – ?Tithonian)
Ctenidodinium	3 – 4	0 – 1	6	6	6	1	1	0 – 1 p v	CRESTS	CINGULAR	HIGH CREST POSTERIOR TO CINGULUM NO CREST ON ANTERIOR SIDE	PROXIMOCHORATE	M – U Jurassic (Callovian – Oxfordian)
Acanthogonyaulax	3 – 4	0 – 1	6	6	6	1	1	—	LINES OF SPINES	PRECINGULAR	GENERAL SPINE COVER	PROXIMATE	U Jurassic (Oxfordian – Kimmeridgian)
Wanaea		Not determined in detail							LOW RIDGES EXCEPT ALONGSIDE CINGULUM	CINGULAR	HIGH FRINGE LIKE CRESTS BORDERING CINGULUM	PROXIMOCHORATE	U Jurassic (Oxfordian – Tithonian)
Pluriarvalium	?5	2	6	?6	6	1	1	1 p v, up to 7 posterior circle plates	LOW RIDGES	? BY LOSS OF ANTERIOR VENTRAL SURFACE	—	PROXIMATE	U Jurassic (U Oxfordian)
Leptodinium	4	0	6	5 – 6	5	1	1	—	CRESTS OR LINES OF SPINES (HEIGHT LESS THAN 1/4 SHELL DIAMETER)	PRECINGULAR	—	PROXIMATE	U Jurassic (Oxfordian) – Oligocene
Belodinium		Not determined in detail							DELICATE CRESTS	APICAL	APICAL HORN ANTAPICAL PERICOEL	PROXIMATE	U Jurassic (Tithonian)
Dichadogonyaulax	3 – 5	0 – ?1	6	6	5 – 6	1	1	Ventral plates sometimes present	CRESTS OR LINES OF SPINES	EPITRACTAL	—	PROXIMATE	U Jurassic (Portlandian)
Heslertonia	3 – 4	0 – 1	6	6	6	1	1	0 – 1 p v	VERY HIGH CRESTS (GREATER THAN 1/4 SHELL DIAMETER)	PRECINGULAR	—	CHORATE	L – U Cretaceous (Hauterivian – Cenomanian)
Heliodinium	?3	?0	6	?0	6	?0	1	—	DAGGER LIKE SPINES ARISING FROM LOW CRESTS	PRECINGULAR	SUTURAL SPINES FLAT FLEXIBLE	PROXIMOCHORATE	L – U Cretaceous (Hauterivian – Cenomanian)
Hystrichodinium		Not determined in detail							LONG SPINES ARISING FROM POSITIONS OF SUTURES	PRECINGULAR	SUTURAL SPINES ROUNDED STIFF	PROXIMOCHORATE	L – U Cretaceous (Hauterivian – Senonian)
Carpodinium	?	?6	6	?	6	?	?	—	CRESTS	PRECINGULAR		PROXIMATE	U Cretaceous (Aptian – Albian)
Microdinium	1	0 – ?1	6	6	6	1	1	Ventral plates sometimes present	LOW CRESTS OR LINES OF SPINES	APICAL	EPITRACT SMALLER THAN HYPOTRACT	PROXIMATE	L – U Cretaceous (?U Aptian – Turonian)
Xiphophoridium	?4	1	6	?6	6	0 – 1	1	—	VERY HIGH CRESTS ESPECIALLY BORDERING CINGULUM	APICAL	—	PROXIMOCHORATE	L – U Cretaceous (?U Aptian – Cenomanian)
Psaligonyaulax	3 – 4	1	6	6	6	1	1	—	CRESTS	PRECINGULAR	APICAL AND ANTAPICAL PERICOELS	BICAVATE	U Cretaceous (Cenomanian) – Tertiary
Hystrichosphaeropsis	?3 – 4	?1	6	6	6	1	1		[illegible]	PRECINGULAR	APICAL AND ANTAPICAL PERICOELS	BICAVATE	[illegible] Tertiary
Raphidodinium		Not determined in detail							LOW BEARING FEW VERY LONG SPINES	NOT REPORTED	SPINES STIFF UP TO TWICE SHELL LENGTH	CHORATE	U Cretaceous
Glyphanodinium	?1	0	5	6	6	1	1	1 p v	LOW CRESTS	APICAL	EPITRACT SMALLER THAN HYPOTRACT	PROXIMATE	Paleocene
Eisenackia	2 – 3	0	6	?6	6	2	1	Ventral plates sometimes present	FOSSAE	APICAL	—	PROXIMATE	Paleocene – L Eocene

Characteristics and stratigraphical distribution of fossil Dinoflagellate cyst genera having a tabulation according with the *Gonyaulax* pattern

VII. FOSSIL DINOFLAGELLATE CYSTS ATTRIBUTED TO *BALTISPHAERIDIUM*

By R. J. DAVEY, C. DOWNIE,
W. A. S. SARJEANT & G. L. WILLIAMS

INTRODUCTION

The genus *Baltisphaeridium* was proposed by Eisenack (1958 : 398) to accommodate species of fossil microplankton having spherical to oval, nontabulate shells bearing simple or branching appendages, consistently closed distally. The type species selected was the Silurian species *B. longispinosum*, having a size range of 40 to 75μ. Eisenack did not compare his new genus with the existing genus *Micrhystridium* Deflandre 1937 (defined as having a shell diameter inferior to 20μ) : subsequent workers, however, assumed a separation between the two genera on the basis of the size restriction of *Micrhystridium*.

Staplin (1961 : 408) proposed the redefinition of *Micrhystridium* by restricting it to forms having appendages closed distally and by removing the size restriction ; this redefinition made *Baltisphaeridium* into a junior synonym of *Micrhystridium*. This proposal was attacked by Eisenack (1962 : 96) and Downie & Sarjeant (1963 : 83–84) ; the latter authors, while recognizing the arbitary nature of the upper size limit of *Micrhystridium*, nevertheless considered that this genus expressed a natural morphological grouping distinct from *Baltisphaeridium*. They proceeded to give an emended diagnosis for *Baltisphaeridium*, as follows :

" Hystrichospheres with spherical to oval shells not divided into fields or plates, bearing ± numerous processes, simple, branching or ramifying, hollow to solid, always with closed tips. The processes are not connected together distally and no outer shell, complete or incomplete, is present : the processes are most often of a single basic type, but processes of two or more types may be present. Mean and modal diameter of the shell greater than 20μ."

At this date, separation of acritarchs from dinoflagellate cysts had not been made. Within the genus *Baltisphaeridium*, there were placed forms having pylomes ; forms with archaeopyles, variously situated ; and forms having no openings of any kind. Thus, within a single genus, there were classed together both species of demonstrable dinoflagellate affinity and morphologically similar forms of unproven and perhaps quite different affinity.

An attempt is here made to remedy this confused situation. Species having spheroidal to ovoidal shells with apical archaeopyles, with the processes arranged so as to give a reflected tabulation 4′, 0a, 6″, 6c, 6‴, 1p, 3⁗, are placed into the new genus *Surculosphaeridium*. Species having a spheroidal to ovoidal shell with an apical archaeopyle, but having numerous processes and an undetermined or intermediate tabulation, are placed in a second new genus, *Cleistosphaeridium*. Species having an elongate ovoidal to ellipsoidal shell, with an apical archaeopyle and processes arranged into distinct rows, are placed in a third new genus *Prolixosphaeridium*. Species having a precingular archaeopyle are placed in a fourth new genus *Exochosphaeridium*. The residue of species, either with a circular pylome (such as the type species, *B. longispinosum*) or with no observed opening, are considered to be acritarchs and left

within the genus *Baltisphaeridium*. A full restudy of this latter genus has recently been published by Staplin, Jansonius & Pocock (1965) ; a consideration of their revisions and proposals is outside the scope of the present paper.

The Species ***hirsutum*** (Ehrenberg) and ***striolatum*** (Deflandre).

Ehrenberg (1838) recorded the occurrence, in Cretaceous flints from Delitzsch, Saxony, of microplankton having simple, oval shells bearing a scatter of simple spines of moderate length. These he named " *Xanthidium hirsutum*(?) ", thus implying their identity with a modern Desmid, now designated *Staurastrum hirsutum* (Ehr.) Ralfs 1848.

Reade (1839) illustrated under this name two quite distinct Upper Cretaceous forms, one having a scatter of long, stout, simple spines, the other a dense matte of very short, fine spines ; neither resembles Ehrenberg's figures at all closely. The second of Reade's forms was also figured, again as *X. hirsutum*, by White (1842) and has subsequently been designated a distinct species, *Baltisphaeridium whitei* (Deflandre & Courteville 1939) Downie & Sarjeant 1963.

Pritchard (1841 : 187, pl. 12, fig. 512) figured as *X. hirsutum* a fourth morphologically distinct form from the Upper Cretaceous globular, and with a very sparse cover of short, stout spines. This clearly represents a distinct species, but it has not been redescribed and the holotype is lost.

In 1932, O. Wetzel illustrated a form from the Baltic Upper Cretaceous, which he named *Hystrichosphaera hirsuta* forma *minor* (pl. 3, fig. 13) ; this was described and refigured by him (1933 : 91, pl. 4, fig. 26). It was of small size (shell diameter 24–28μ) with numerous (50–60) simple, stout spines of moderate length, quite comparable to Ehrenberg's figure. Forms from the Dutch Upper Cretaceous were described and figured as forma *minor* by de Wit (1943 : 381–83) ; his text-figure 9*a* corresponds broadly to Wetzel's description, but his text-figure 9*b* shows a form with very numerous, extremely abbreviate spines, quite unlike Wetzel's description and constituting yet a sixth morphological type!

Wetzel also described and figured a second form, which he named *H.* cf. *hirsuta* forma *varians* (1932, pl. 3, fig. 11 ; 1933 : 93, pl. 4, figs. 27–29). This has quite long spines, sometimes branching at their tips, and a shell surface bearing a pattern of low ridges. One of his figures (pl. 4, fig. 29) indicates possession of an archaeopyle. Forms from the Dutch Upper Cretaceous were figured under this name by de Wit (1943, text-fig. 10*a*, *b*).

In 1937, Deflandre transferred the species *hirsutum* to his genus *Hystrichosphaeridium*, commenting : " It is quite certain that neither of the forms described by O. Wetzel . . . corresponds to the species of Ehrenberg.". He suggested, but did not firmly propose, elevation of forma *minor* to specific status, as *Hystrichosphaeridium minor*. In the same paper, a new Upper Cretaceous species was described, having a surface divided into more or less triangular, concave fields and bearing appendages of very variable character (relatively slender, simple or branching spines, together

with broader processes, branching strongly and with tips secondarily branched), the bases of adjacent appendages being connected by striae on the shell surface. This was named *Hystrichosphaeridium striolatum* (Deflandre 1957 : 72, pl. 15, figs. 1, 2); it was again figured by Deflandre & Courteville (1939, pl. 3, fig. 2).

In 1941, Maria Lejeune-Carpentier re-examined Ehrenberg's material and relocated the holotype ; it is contained in Slide XXVI of his series " Feuerstein von Delitzsch " and is in the Institut für Paläontologie und Museum der Humboldt-Universität, Berlin ; it is labelled in pencil " *X. hirtum* ", obviously in error. Lejeune-Carpentier comments wryly : " C. G. Ehrenberg published . . . only a very rough drawing, as likely to mislead his successors as to guide them." Her re-examination showed the shell surface to be divided into striated fields ; the appendages were normally simple and several were found to be " united in pairs by a sort of web." She concluded : " What seems certain is the identity of *H. striolatum* Defl. with Ehrenberg's species " and she retained the name *hirsutum* for this conjoint species.

De Wit (1944) figured a form from the Dutch Upper Cretaceous as *H. hirsutum* (unnumbered text-figure). This had simple, stiff spines : it closely resembled one of the forms he had previously figured (1943, text-fig. 10*a*) as *H. hirsutum* forma *varians* and also resembled Ehrenberg's figures, but the species represented does not accord with Lejeune-Carpentier's redescription of the holotype.

In 1946, Deflandre discussed the taxonomic position and commented : " The figure of Ehrenberg . . . has as legend " *X. hirsutum* (?) from a flint from Delitzsch," *X. hirsutum* (without ?) being given as ' living at Berlin ' . . . It is thus not possible now to utilize the name *X. hirsutum* Ehr. and to make of it a *Hystrichosphaeridium hirsutum* (Ehr.), as Maria Lejeune-Carpentier wishes and . . . with very diverse meanings. The microfossil rediscovered at Berlin, whether or not it served as a model for Ehrenberg, being, according to Mme. Lejeune-Carpentier, identical to *H. striolatum* Defl., must thus be catalogued under this latter name."

Deflandre's comments and proposals are wholly correct. However, in 1948, André Pastiels described Eocene forms from Belgium under the names *Hystrichosphaeridium* cf. *hirsutum* Ehrbg. and *H.* cf. *hirsutum* forma *minor*. Subsequently Cookson (1953) described an Australian Tertiary form as *H.* cf. *hirsutum* : and Cookson & Eisenack (1958) applied this name to globular forms with short, simple spines from the Lower Cretaceous of Australia and Papua. In 1960, Klement, mentioning this form in discussion, transferred it to the genus *Baltisphaeridium*. A further complication was introduced by W. Wetzel (1952 : 401). On the basis that Ehrenberg's type specimen, when re-located by Lejeune-Carpentier, bore the manuscript name *H. hirtum* (interpreted by her as an accidental mis-spelling), he employed the name *Hystrichosphaeridium hirtum* for forms from the Baltic Danian. He figured three forms as " *H.* cf. *hirtum* " (1952, text-figs. 17–19). One of these is spherical, with moderately long, simple spines (text-fig. 17) ; the second (text-fig. 18) is oval in outline, with simple spines of moderate length ; and the third (text-fig. 19) is also ovoidal, with long, simple or branching spines. The two latter forms are in fact more comparable to *Prolixosphaeridium xanthiopyxides* (Deflandre). Wetzel

further complicated matters by designating other forms " *H.* cf. *striolatum* " (pp. 399–400, text-figs. 13, 14) : both forms show " archaeopyles ", but neither appears truly comparable to Deflandre's species.

In a second paper describing Danian assemblages, Wetzel (1955 : 38, text-fig. 11) reiterated his proposals and described a new form, under the name *H. hirtum* subsp. *amplum*. The text-figure shows a spherical form with short, stiff spines, again more approaching Ehrenberg's text-figure than the specimen as redescribed.

The name *striolatum* has been employed in equal measure—by Valensi (1955 : 593, pls. 4, fig. 10 ; pl. 5, fig. 3) in describing French Cretaceous forms from Magdalenian worked flints ; by Gocht (1959 : 73, pl. 7, fig. 10) who described forms from the German Lower Cretaceous as *H.* cf. *striolatum* ; and by Górka (1963 : 68–70, pl. 10, fig. 6–7, text-pl. 8, figs. 5–6) who used the same name to designate forms from the Upper Cretaceous of Poland.

Downie & Sarjeant (1963, pp. 91–2) compromized by including both names (*hirsutum* and *striolatum*) in their list of species attributable to *Baltisphaeridium*. Similarly, both names figure in their list of valid taxa (Downie & Sarjeant 1964: 91, 97). In the latter work, *hirtum* is listed as an invalid alteration of *hirsutum* (p. 166).

The present situation thus remains confused. One of the authors (R.J.D.) was permitted, through the courtesy of Prof. Deflandre, to make a full re-examination of the holotype of *striolatum* which confirmed that Ehrenberg's and Deflandre's species are conspecific. For the reasons enunciated by Deflandre (1946), the species must be designated *striolatum*. The name *hirtum*, whether or not originally written in error, was merely pencilled on to a slide by Ehrenberg and was not validly published until 1952. It is therefore either an invalid alteration of the name *hirsutum* or a junior synonym of *striolatum* ; however regarded, it cannot be retained.

The holotype of the species *striolatum* (in the laboratoire de Micropléontologie, École Pratique des Hautes Études, Paris, preparation AH 89, flint S.52) is contained in a flint flake. It is here provisionally included in the new genus *Exochosphaeridium*, on the basis of similarity in general structure to the type species, *E. phragmites*. However, the apical process characteristic of the genus was not certainly observed, nor was an archaeopyle noted.

In view of the highly doubtful character of the morphology of the three subspecies *amplum* W. Wetzel, *minor* O. Wetzel and *varians* O. Wetzel, it is considered that their erection to specific status would be inappropriate until a full restudy of the holotypes has been undertaken. They are therefore provisionally regarded as subspecies of *E. striolatum*.

Genus ***SURCULOSPHAERIDIUM*** nov.

Derivation of name. Latin, *surculus*, branch or twig ; *sphaera*, a ball—with reference to the branched nature of the processes radiating from the central body.

DIAGNOSIS. Subspherical chorate cysts bearing a moderate number of intratabular processes, considered to reflect the tabulation 4′, 6″, 6c, 6‴, 1p, 3⁗. Processes solid, closed distally and branched. Archaeopyle apical.

TYPE SPECIES. *Hystrichosphaeridium cribrotubiferum* Sarjeant 1960. Upper Jurassic (*Cardioceras cordatum* Zone) ; England.

REMARKS. The processes usually show a distinct circular arrangement on the surface of central body. The cingular processes are distinctive, being deeply furcate, and with the archaeopyle make orientation easy.

Surculosphaeridium cribrotubiferum (Sarjeant)

Pl. 9, fig. 6 ; Text-fig. 41

1960. *Hystrichosphaeridium cribrotubiferum* Sarjeant : 137, pl. 6, figs. 2, 3, text-fig. 1.

EMENDED DIAGNOSIS. Subspherical central body bearing moderate number of solid, distally closed, perforate processes. Processes variably branched, sometimes deeply, especially cingular processes. Processes reflect a tabulation of 4′, 6″, 6c, 6‴, 1p, 3⁗.

HOLOTYPE. B.M.(N.H.) slide V.51735(1). Upper Jurassic (Oxford Clay, *Cardioceras cordatum* Zone) ; England.

DIMENSIONS. Holotype : overall diameter 75μ, diameter of central body 43 by 39μ, length of processes up to 24μ. Range : overall diameters 60–80μ. Number of specimens measured, 8.

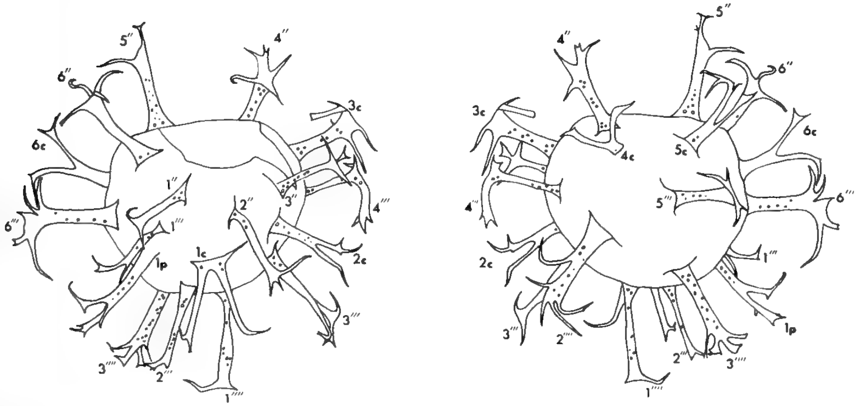


FIG. 41. *Surculosphaeridium cribrotubiferum* (Sarjeant). Holotype. Tabulation as reflected by the processes. Left, oblique ventral view ; right, oblique dorsal view. × c. 600.

REMARKS. The diagnosis of this species has been emended to draw attention to the closed processes, which reflect a definite tabulation characteristic of the genus and the presence of an archaeopyle. The processes were originally considered to be open distally ; however, full re-examination of the holotype at high magnifications has not confirmed this.

Surculosphaeridium vestitum (Deflandre)

Pl. 9, fig. 8 ; Text-fig. 42

1938. *Hystrichosphaeridium vestitum* Deflandre : 189, pl. 11, figs. 4–6.
1938. *Hystrichosphaeridium vestitum* Deflandre ; Deflandre : 688, text-fig. 3.
1947. *Hystrichosphaeridium vestitum* Deflandre ; Deflandre, text-fig. 1, no. 3.
1952. *Hystrichosphaeridium vestitum* Deflandre ; Deflandre, text-fig. 7.
1955. *Hystrichosphaeridium vestitum* Deflandre ; Valensi : 587, pl. 2, fig. 8.
1960*c*. *Baltisphaeridium vestitum* (Deflandre) Sarjeant : 397, pl. 13, fig. 8, pl. 14, figs. 13, 14.
1962*a*. *Baltisphaeridium vestitum* (Deflandre) : Sarjeant, pl. 12, figs. 3, 5, 6.

REMARKS. The holotype, from the Oxfordian of France, has been restudied by two of the authors (R.J.D. and W.A.S.S.), through the courtesy of Prof. Deflandre ; and the specimens figured by Sarjeant (1962*a*) from the Oxfordian of England have also been re-examined in the light of recent studies. The processes of this species are extremely variable in form, so making the elucidation of the reflected tabulation very difficult. The processes are intratabular, the larger ones reflecting one plate of the original dinoflagellate theca, while some of the finer ones, in contrast, occur in twos and threes and represent a larger process which has been subdivided down to the surface of the central body. Thus two or three of these processes may reflect a single plate. The most distinctive and characteristic processes are the ones lying in the cingular zone. These are either deeply furcate or completely divided into two finer

FIG. 42. *Surculosphaeridium vestitum* (Deflandre). Position of cingular processes. Left, dorsal view ; right, ventral surface by transparency. V.51736(1). × c. 650.

processes. Such cingular processes are especially characteristic of the genus *Surculosphaeridium*, and make specimen orientation comparatively easy. The form of the processes and the exact distribution of the non-cingular processes, although difficult to determine, indicate that this species does belong to this genus.

MATERIAL (figured). B.M.(N.H.) slide V.51736(1). Lower Oxfordian, Dorset, England. Upper Jurassic, England.

DIMENSIONS. Figured specimen : diameter of central body 37 by 47μ, length of processes up to 30μ.

Surculosphaeridium longifurcatum (Firtion)

Pl. 8, figs. 7, 11, Text-figs. 43, 44

1952. *Hystrichosphaeridium longifurcatum* Firtion : 157, pl. 9, fig. 1 ; text-fig. 1, H, K, L and M.

1963. *Baltisphaeridium longifurcatum* (Firtion) Downie & Sarjeant : 91,

DESCRIPTION. A number of specimens have been found in the British Cenomanian which appear to be comparable to Firtion's species from the Cenomanian of France.

The central body is subspherical. The periphragm is smooth and gives rise to a more or less constant 26 processes in a complete specimen. An angular archaeopyle is commonly present, the detached apical region bearing 4 apical processes. The processes are closed distally and are rather variable in form, being simple, lobate foliate or digitate. Some of the processes, particularly those marking the cingulum, are deeply branched. In the Upper Cenomanian particularly, the cingular processes, each reflecting a cingular plate, may be completely subdivided. Thus there appears to be two instead of one cingular process for each plate.

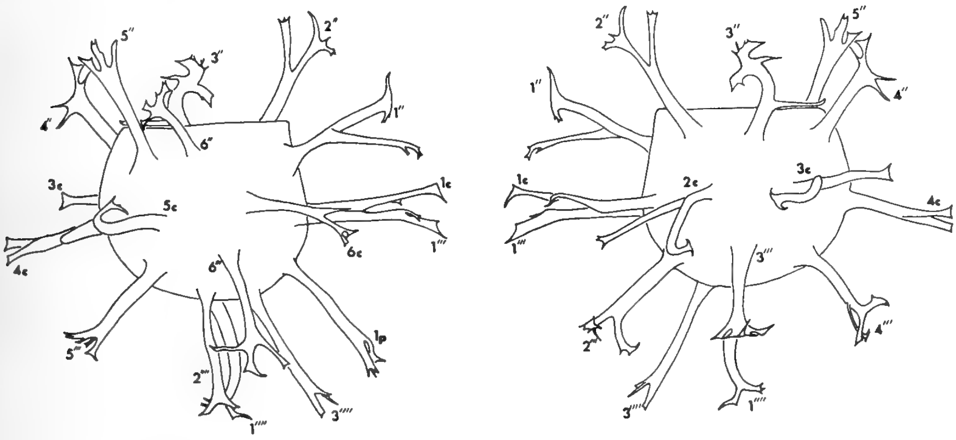


FIG. 43. *Surculosphaeridium longifurcatum* (Firtion). Tabulation as reflected by the processes. Left, top lateral view ; right, bottom lateral view. PF.3042(1). × c. 800.

The presence of an apical archaeopyle and the distinctive deeply furcate cingular processes make orientation of this species relatively easy. A number of well preserved specimens were studied and from the positions of the intratabular processes the reflected tabulation appeared to be 4′, 6″, 6c, 6‴, 1p, 3⁗. The test of the original dinoflagellate is tentatively reconstructed in the accompanying figure (Text-fig. 41).

The reflected tabulation of *S. longifurcatum* is the same as in *S. cribrotubiferum* (Sarjeant, 1960); however, the latter possesses characteristically perforate processes.

MATERIAL (Figured). Pl. 8, fig. 11, Geol. Surv. Colln. PF.3042(1). Lower Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey at 840 feet depth. Upper Cretaceous (Cenomanian). Another specimen, Pl. 8, fig. 7, FM.730/2, at 730 feet depth.

DIMENSIONS. Figured specimens: diameter of central body 32 by 37μ, length processes 20–24μ. Range, lateral view: diameter of central body 30–47μ; apical view: diameter of central body 36–50μ; length of processes 14–29μ. Mean diameter of archaeopyle, 20μ. Number of specimens measured, 24.

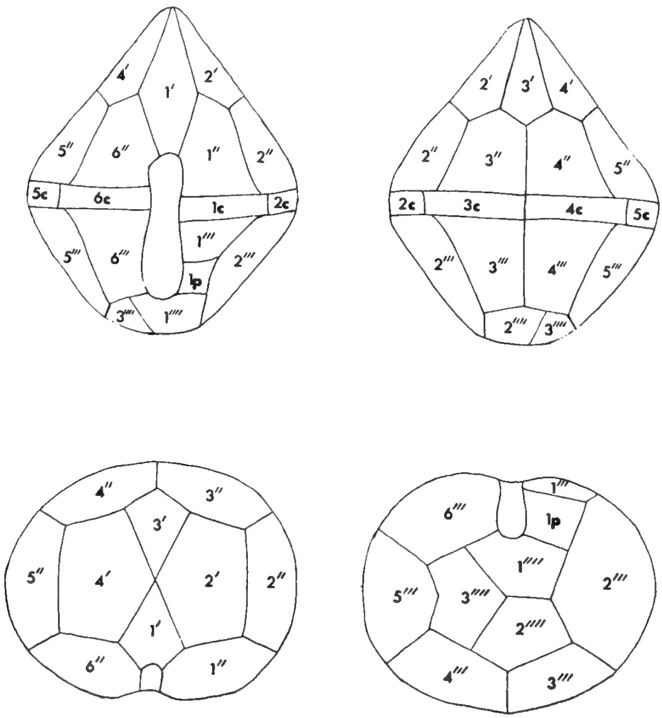


FIG. 44. *Surculosphaeridium longifurcatum* (Firtion). The probable original tabulation of the dinoflagellate.

Genus *EXOCHOSPHAERIDIUM* nov.

DERIVATION OF NAME. Greek, *exochos*, projecting or prominent ; *sphaera*, ball—with reference to the distinctive nature of the apical process.

DIAGNOSIS. Subspherical chorate cysts bearing numerous, commonly simple, closed processes. Apical process larger than normal processes and irregularly branched. Archaeopyle precingular.

TYPE SPECIES. *Exochosphaeridium phragmites* sp. nov. Upper Cretaceous (Cenomanian) ; England.

REMARKS. The processes are commonly acuminate, often joining proximally, but may be branched. Only rarely can any alignment of these processes be observed. The apical process makes orientation easy and indicates that the archaeopyle is precingular. Detached archaeopyle plates have been found and these show the characteristic precingular shape.

Exochosphaeridium phragmites sp. nov.

Pl. 2, figs. 8—10

DERIVATION OF NAME. Latin, *phragmites*, a reed—with reference to the reed-like shape of the processes of this species.

DIAGNOSIS. Central body subspherical to oval, possessing a pitted surface and bearing numerous acuminate processes. Processes solid or fibrous, broad-based, bases of adjacent processes often confluent. Distinctively branched apical process present and commonly a precingular archaeopyle.

HOLOTYPE. Geol. Surv. Colln. PF.3035(3). Lower Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey at 840 ft. depth. Upper Cretaceous (Cenomanian).

PARATYPE. Geol. Surv. Colln. PF.3043(1). H.M. Geological Survey Borehole, Fetcham Mill, Surrey at 810 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype : diameter of central body 49 by 56μ, length of processes up to 22μ. Paratype : diameter of central body 33 by 36μ, length of processes up to 22μ.

DESCRIPTION. The fibrous processes may occasionally be slightly perforate. Division of a process into two often takes place medially, and more rarely distally. The processes may terminate distally in a point or may be blunted. The arrangement of the processes usually appears to be haphazard and in only one specimen, the paratype, can any alignment be observed. In this specimen a definite alignment can be seen on both sides of the cingulum running parallel to this structure. An apical process and an archaeopyle are present, thus making orientation easy. The apical process is very distinctive, being foliate in shape ; it is situated near the edge of the archaeopyle. The position of this process indicates that it must be an apical process and that the archaeopyle is precingular. *E. phragmites* occurs throughout the Cenomanian of England.

REMARKS. Superficially *E. phragmites* resembles *Baltisphaeridium striolatum* Deflandre, the holotype of which was examined by one of the authors (R.J.D.) by kind permission of Professor Deflandre. *B. striolatum*, however, has a definitely striated periphragm on the surface of the central body and neither a distinctive apical process nor an archaeopyle has been observed. It must be made clear, however, that the holotype of *B. striolatum* is extremely dark and the lower surface, which may possess an archaeopyle and an *apical* process, is not observable.

OTHER SPECIES

The following species are here included in *Exochosphaeridium* gen. nov. on the basis of similarity in structure and process pattern :

Exochosphaeridium palmatum (Deflandre & Courteville 1939). Upper Cretaceous ; France.

Exochosphaeridium striolatum (Deflandre 1937*a*). Upper Cretaceous ; France.

The following species is tentatively referred to this genus, subject to subsequent confirmation of the precingular position of the archeopyle :

?*Exoxhosphaeridium pseudhystrichodinium* (Deflandre 1937*a*). Upper Cretaceous ; France.

Genus ***CLEISTOSPHAERIDIUM*** nov.

DERIVATION OF NAME. Greek, *kleistos*, shut, closed ; *sphaera*, ball—in reference to shell shape and the closed nature of the processes.

DIAGNOSIS. Chorate dinoflagellate cysts having spherical to ovoidal central bodies bearing numerous processes, typically closed distally and without communication to endocoel. Number of processes typically exceeding 50 ; processes showing no definite alignment, so that the tabulation is not determinable. Archaeopyle apical, with zigzag margin.

TYPE SPECIES. *Cleistophaeridium diversispinosum* sp. nov. Eocene ; England.

REMARKS. It is not clear whether the processes of this genus are intertabular or intratabular ; nor is there any differentiation between processes which would enable the establishment of orientation. The shape and size of the archaeopyle, however, strongly suggests that it is apical.

All Mesozoic and Tertiary species, formerly attributed to *Baltisphaeridium*, which show an apparent apical archaeopyle and which cannot be related to *Surculosphaeridium* or *Prolixosphaeridium*, are provisionally reattributed to this genus. Species are included whose process numbers are relatively low ; it is probable that re-examination of these will necessitate their removal to other genera as soon as the reflected tabulation is determined.

Cleistosphaeridium diversispinosum sp. nov.

Pl. 10, fig. 7

DERIVATION OF NAME. Latin, *diversus*, different ; *spinosus*, thorny—with reference to the variable shape of the processes.

DIAGNOSIS. A *Cleistospharidium* with granular wall and polygonal archaeopyle. Processes solid, taeniate or tubular, usually slender and proximally expanded. Distal end forked or expanded.

HOLOTYPE. B.M.(N.H.) slide V.51750(1). Eocene (London Clay) ; Whitecliff.

DIMENSIONS. Holotype : diameter of body 38μ, length of processes, 9–16μ. Observed range : diameter of body 38–43μ, length of processes 7–23μ. Number of specimens measured, 5.

DESCRIPTION. This species is distinguished by the variable nature of the process ends. The expanded termination may be bifurcate, orthogonal or patulate, one branch may be larger than the other. The edges are usually denticulate and the processes may be up to 5μ wide ; but are usually about 2μ. There is more than one process to a plate.

OCCURRENCE. London Clay ; Whitecliff, Enborne and Sheppey.

REMARKS. Only *Cleistosphaeridium pectiniforme* (Gerlach) 1961 comb. nov. resembles *C. diversispinosum* to any degree. It has widely forked processes with spinose margins ; it does not, however, have the variability of process ending shown by our species. The species *pectiniforme* is reattributed to the genus *Cleistosphaeridium* provisionally on the basis of its similarity to *C. diversispinosum*, despite lack of knowledge of its mode of archaeopyle formation.

Cleistosphaeridium ancoriferum (Cookson & Eisenack)

Pl. 9, fig. 1

1960*a*. *Hystrichosphaeridium ancoriferum* Cookson & Eisenack : 8, pl. 2, fig. 11.
1964. *Hystrichosphaeridium ancoriferum* Cookson & Eisenack ; Cookson & Hughes : 47, pl. 9, fig. 7.

DESCRIPTION. The specimens of *C. ancoriferum* found in the Lower Cenomanian of England, first described and figured by Cookson & Hughes (1964) strongly resemble those examples recorded from Australia (Cookson & Eisenack, 1960*a*). Many of the specimens from the Fetcham Mill Borehole possess a 6-sided apical archaeopyle the shape of which is often difficult to determine due to distortion. However, detached apical regions are relatively abundant. The processes are hollow, the cavity often being constricted to some extent, and closed distally and proximally. They do not appear to be aligned to any noticeable extent.

C. ancoriferum has been recorded from the Albian and Cenomanian of England and Australia.

MATERIAL (figured). Geol. Surv. Colln. slide PF.3044(1). Lower Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey, at 810 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Figured specimen : diameter of central body 32 by 41μ, length of processes up to 9μ. Range : diameter of central body 20–45μ, length of processes up to 9μ. Number of specimens measured, 30.

REMARKS. As with Cookson & Hughes (1964), difficulty was met with when trying to distinguish *C. ancoriferum* from *Chlamydophorella nyei* (Cookson & Eisenack 1958), since the outer membrane and apical prominence of the latter are often obscure. The processes of *C. nyei*, however, are finer and shorter than those of *C. ancoriferum.*

Cookson & Eisenack (1960*a*) comment on the " transparent tips " of the processes of *C. ancoriferum.* The cavities are in fact closed by a thin, tranparent membrane. This character may well indicate a close relation to *Chlamydophorella.* The species *Cleistosphaeridium ancoriferum* may have arisen by the progressive restriction of a formerly continuous membrane ; or alternatively, *Chlamydopherella* may have arisen by the extension of a membrane which originally merely tipped the processes.

Cleistosphaeridium heteracanthum (Deflandre & Cookson)

Pl. 2, figs. 6, 7

1955. *Hystrichosphaeridium heteracanthum* Deflandre & Cookson : 276, pl. 2, figs. 5, 6 ; text-figs. 40, 41.
1961*a*. *Hystrichosphaeridium heteracanthum* Deflandre & Cookson ; Cookson & Eisenack : 73, pl. 12, fig. 14.
1963. *Baltisphaeridium heteracanthum* (Deflandre & Cookson) Downie & Sarjeant : 91.

REMARKS. The Cenomanian specimens from England are very similar to the forms illustrated by Deflandre & Cookson (1955) from the Upper Cretaceous of Victoria, Australia.

The surface of the central body may be smooth or reticulate. The processes are extremely variable in shape but do not vary markedly in length. One complete specimen has been found and this possessed one large distinctive process. In all the other studied examples this process was absent and there was, in every case, a large, well defined, archaeopyle. It is probable, therefore, that the process is apical and that the archaeopyle, when developed, is also apical in position. Alignment of the processes on the surface of the central body has not been observed. Some difficulty was experienced in distinguishing *C. heteracanthum* from *C. multifurcatum* (Deflandre). The processes of the latter, however, appear to be considerably less varied, most of them terminating with a simple bifurcation or being blunted.

C. heteracanthum is found throughout the Cenomanian of England, and in Australia it has been recorded from the Upper Cretaceous and Lower Eocene.

One specimen of *C. heteracanthum* illustrated by Deflandre & Cookson (1955, pl. 12, fig. 14) appears to possess an apical archaeopyle. For the latter reason this species is tentatively placed in the genus *Cleistosphaeridium.*

MATERIAL (figured). Pl. 2, fig. 6, Geol. Surv. Colln. slide PF.3041(2). Lower Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey, at 650 feet depth. Upper Cretaceous (Cenomanian). Another specimen, Pl. 2, fig. 7, at 840 feet depth.

DIMENSIONS. Figured specimens : diameter of central body 52 by 59μ, length of processes up to 17μ. Range of Cenomanian specimens : diameter of central body 50–68μ, length of processes up to 17μ. Number of specimens measured, 5.

?*Cleistosphaeridium flexuosum* sp. nov.

Pl. 2, fig. 5

DERIVATION OF NAME. Latin, *flexuosus*, flexuous—with reference to the form of the processes.

DIAGNOSIS. Central body subspherical to elongate, bearing numerous, broadly acuminate, processes. All processes of approximately same length, slightly fibrous and always flexuous.

HOLOTYPE. Geol. Surv. Colln. slide PF.3045(1). Lower Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey at 840 feet depth. Upper Cretaceous (Cenomanian.)

DIMENSIONS. Holotype : diameter of central body 29 by 37μ, length of processes up to 17μ. Range : diameter of central body 20 to 45μ, length of processes up to 20μ. Number of specimens measured, 4.

DESCRIPTION. The most distinctive feature of ?*C. flexuosum* is the flexuous nature of the broad fibrous processes. The nature of the surface of the central body is difficult to determine and the presence of an archaeopyle has not been recorded.

This is a rare species throughout the Cenomanian of England.

REMARKS. The nature of the processes easily differentiate ?*C. flexuous* from all previously described species. This species is tentatively placed in *Cleistosphaeridium* on the general form of the central body and processes.

Cleistosphaeridium disjunctum sp. nov.

Pl. 11, fig. 9

DERIVATION OF NAME. Latin, *dis*, asunder ; *junctus*, joined.

DIAGNOSIS. A *Cleistosphaeridium* with granular central body and polygonal archaeopyle. Numerous processes hollow, unbranched, closed distally and proximally, with distal terminations blunt, acuminate, or bearing small spines. Processes regularly arranged.

HOLOTYPE. B.M.(N.H.) slide V.51739(2). Eocene (London Clay) ; Whitecliff.

DIMENSIONS. Holotype : diameter of central body 47–54μ, length of processes 10–15μ. Observed range : diameter of body 30–56μ, process length 10–19μ. Number of specimens measured, 13.

DESCRIPTION. Attempts to make subdivisions on the type and pattern of processes have been fruitless ; the species is a very variable one. The wall also shows considerable variation in thickness.

The processes are from a quarter to a half of the body diameter and are hollow. The process length in an individual is constant, as are the process terminations. The number of processes exceeds 50. Plates can be recognized on damaged specimens and the number of processes ranges from four to seven on each plate.

OCCURRENCE. London Clay ; Whitecliff and Enborne.

REMARKS. *C. disjunctum* resembles *Baltisphaeridium densicomatum* (Maier) which however splits equatorially and sometimes has forked processes. *B. iaculigerum* Klement has longer processes and the archaeopyle is unknown.

In view of the regular arrangement of the processes, a feature not typical of the genus, the allocation of this species to *Cleistosphaeridium* must be regarded as provisional.

OTHER SPECIES

The following species, formerly attributed to *Baltisphaeridium*, are here provisionally reattributed to *Cleistosphaeridium* gen. nov., on the basis of their apparent possession of an apical archaeopyle and in absence of knowledge of their reflected tabulation (if any). Species of especially doubtful character are differentiated with a question mark :

Cleistosphaeridium ashdodense (Rossignol 1962). Miocene ; Australia.

?*Cleistosphaeridium danicum* (W. Wetzel 1952). Paleocene (Danian) ; Baltic.

Cleistosphaeridium echinoides (Maier 1959). Oligocene ; Germany.

Cleistosphaeridium ehrenbergi (Deflandre 1947*b*). Upper Jurassic ; France.

Cleistosphaeridium israelianum (Rossignol 1962). Quaternary ; Israel.

Cleistosphaeridium leve (Maier 1959). Oligocene–Miocene ; Germany.

Cleistosphaeridium lumectum (Sarjeant 1960*a*). Upper Jurassic ; England.

Cleistosphaeridium machaerophorum (Deflandre & Cookson 1955). Miocene ; Australia.

Cleistosphaeridium multifurcatum (Deflandre 1937*a*). Upper Cretaceous ; France.

?*Cleistosphaeridium oligacanthum* (W. Wetzel 1952). Paleocene (Danian) ; Baltic.

Cleistosphaeridium pectiniforme (Gerlach 1961). Oligocene ; Germany.

Cleistosphaeridium pilosum (Ehrenberg 1954). Upper Jurassic ; Poland.

Cleistosphaeridium polytrichum (Valensi 1947). Middle Jurassic ; France.

?*Cleistosphaeridium spiralisetum* (de Wit 1943). Upper Cretaceous ; Netherlands.

Cleistosphaeridium tiara (Klumpp 1953). Eocene ; Germany.

Cleistosphaeridium tribuliferum (Sarjeant 1962*b*). Upper Jurassic ; England.

Genus *PROLIXOSPHAERIDIUM* nov.

DERIVATION OF NAME. Latin, *prolixus*, stretched out long ; *sphaera* ball—with reference to the shape of the central body.

DIAGNOSIS. Shell shape elongate ovoidal to ellipsoidal, one pole (apical) typically lost in archaeopyle formation. Opposite pole occupied by one or two antapical processes. Remaining processes arranged in distinct rows encircling test ; these rows slightly offset at a position corresponding to sulcus. Number of processes exceeding 30. Processes closed proximally, closed or open distally : their distal terminations simple ; flaring in varied fashion ; or briefly furcate. Shell surface bearing cover of coarse granules or very short, simple spinelets, or lacking such ornamentation.

TYPE SPECIES. *Prolixosphaeridium deirense*, sp. nov. Lower Cretaceous (Middle Barremian) ; England.

REMARKS. A group of Mesozoic dinoflagellate cysts exhibit an elongate central body with a terminal archaeopyle. Their distinctive character and unity of form merits taxomonic recognition at generic level. The arrangement of the processes suggests that they are intratabular, corresponding perhaps to crest nodes, but prolonged study of many individuals would be necessary before this could be confirmed.

Prolixosphaeridium deirense sp. nov.

Pl. 3, fig. 2 ; Text-fig. 45

DERIVATION OF NAME. Latin, *deirense*, of Deira, the ancient kingdom occupying what is now East Yorkshire.

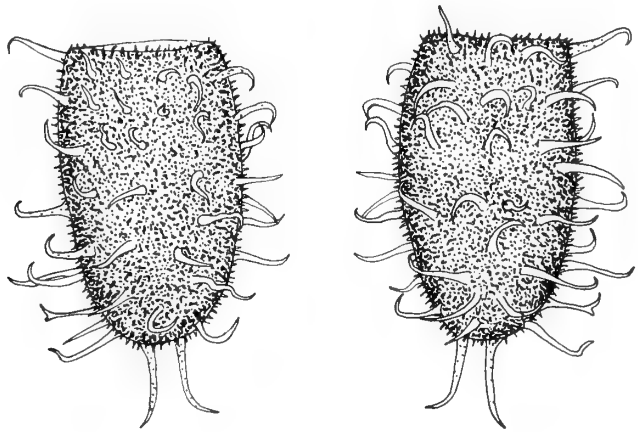


FIG. 45. *Prolixosphaeridium deirense* gen. et sp. nov. Left, ventral view ; right, dorsal view. × c. 1000.

DIAGNOSIS. A *Prolixosphaeridium* having an elongate ovoidal central body bearing 60–65 processes. Processes simple or briefly bifurcate (bifurcations unequally long), closed proximally, dominantly or constantly closed distally. Two processes occupying antapical pole ; remaining processes showing alignment in rows, encircling test and offset at a position corresponding to sulcus. Apex typically lost in archaeopyle formation ; about six rows of processes present between archaeopyle and antapex, gap between third and fourth *row* probably corresponding to cingulum. Test surface granular and bearing dense cover of very short spinelets.

HOLOTYPE. B.M.(N.H.) slide V.51727(2), Speeton Clay, Shell West Heslerton boring, Yorkshire, Lower Cretaceous (Middle Barremian).

DIMENSIONS. Holotype : overall length (apex lacking) 62μ ; overall breadth 46μ ; shell length (apex lacking) 50μ ; breadth 28μ ; spines c.10–12μ long, spinelets 1–1·5μ long. Dimensions of other specimens closely similar.

DESCRIPTION. The distribution of the processes on the epitheca is into three *rows* ; these appear to respectively comprise 9, 10 and 10 processes. Distribution of processes on the hypotheca was less easily determined. Two rows of processes were present posterior to the presumed cingulum, each apparently comprising 9 processes ; and some 9 further processes clustered round the antapex, probably but not certainly representing a sixth process row.

The short spinelets form a stubble on the granular surface of the periphragm.

REMARKS. This species was encountered only in the 39 foot horizon in the West Heslerton Borehole. It closely resembles the Upper Jurassic species *P. mixtispinosum* (Klement 1960), differing in the broader shell shape (length-width ratio of *P. mixtispinosum* consistently greater than 2 : 1, against a length-width ratio in *P. deirense* consistently markedly less than 2 : 1) ; in the furcate character of some processes ; and in the somewhat shorter spinelets. These distinctions are minor ; there can be no doubt that *P. deirense* and *P. mixtispinosum* are closely related.

Prolixosphaeridium granulosum (Deflandre)

1937. *Hystrichosphaeridium xanthiopyxides* var. *granulosum* Deflandre : 29, pl. 16, fig. 4.
1955. *Hystrichosphaeridium xanthiopyxides* var. *granulosum* Deflandre ; Valensi : 594, pls. 3, fig. 7, pl. 5, fig. 16.
1957. *Hystrichosphaeridium xanthiopyxides* var. *granulosum* Deflandre ; Downie : 426, text-fig. 46.
1960. *Baltisphaeridium xanthiopyxides* var. *granulosum* (Deflandre) Klement : 59,
1962*a* *Baltisphaeridium granulosum* (Deflandre) ; Sarjeant : 264, pl. 2, fig. 14, text-fig. 8*c*.

REMARKS. This species, which has a known range from Upper Jurassic to Upper Cretaceous, is represented in the London Clay at Whitecliff and Enborne ; it is, however, possible that these specimens are derived.

It differs from *P. deirense* in having only approximately 30 processes, organized into rows, with one antapical process.

OTHER SPECIES

The following species are here included in the genus *Prolixosphaeridium* nov., on the basis of shape, character of processes and possession of an apical archaeopyle :

Prolixosphaeridium mixtispinosum (Klement 1960). Upper Jurassic ; Germany.

Prolixosphaeridium parvispinum (Deflandre 1937*a*). Upper Cretaceous ; France.

The following species, inadequately described and figured, is doubtfully referred to this genus :

?*Prolixosphaeridium xanthiopyxides* (O. Wetzel 1933). Upper Cretaceous ; Germany.

OTHER MESOZOIC AND CAINOZOIC SPECIES ATTRIBUTED TO *BALTISPHAERIDIUM*

In the preceding section, the bulk of post-Palaeozoic species, hitherto placed in *Baltisphaeridium*, have been reattributed to four new genera on the bases of shape, process arrangement and possession of archaeopyles. The species *Baltisphaeridium spinosum* (White) is considered in the previous chapter ; it is shown to be probably synonymous with *Hystrichodinium pulchrum* Deflandre but since the holotype of *B. spinosum* is lost, restudy is not possible. The abandonment of the name *spinosum* is therefore proposed. The species *Baltisphaeridium geometricum* (Pastiels) was originally placed in the genus *Hystrichosphaeridium* and was then a junior homonym of a species proposed by Deflandre (1945) ; since invalid at the time of publication, this name must be rejected. Pastiel's forms are attributable to the genus *Wetzeliella* and are discussed more fully on p. 192.

The holotypes of the two species, *Baltisphaeridium ferox* (Deflandre) and *B. tridactylites* (Valensi) were re-examined recently by one of the authors (R.J.D.) in consultation with Prof. Deflandre. On the basis of this re-examination, their reattribution to *Hystrichokolpoma* is here proposed. Reattribution of two species, (*Baltisphaeridium neptuni* Eisenack 1958 and *B. triangulatum* Gerlach 1961) to the genus *Achomosphaera* is proposed on pp. 51, 52 ; and in the discussion of the genus *Hystrichosphaeridium* and its allies (see pp. 53–105) the reattribution of two further species to new genera is proposed, *Baltisphaeridium dictyophorum* (Cookson & Eisenack) becoming *Oligosphaeridium* and *B. striatoconus* (Deflandre & Cookson) becoming *Litosphaeridium*.

Five further species currently attributed to the genus *Baltisphaeridium* appear also to merit reattribution. Four species from the German Tertiary, three of them attributed by Maier (1959) to her invalid genus *Galea* and subsequently reattributed by Downie & Sarjeant (1963) to *Baltisphaeridium* (*B. galea* ; *B. lychneum* ; *B. rehdense* ; and *B. twistringense*) are herewith tentatively reattributed to the genus *Areoligera* on the basis of archaeopyle structure. The species *Baltisphaeridium placacanthum* (Deflandre & Cookson) is herewith reattributed to *Systematophora*, since the processes show the grouping characteristic of the latter genus.

A residue of Mesosoic and Tertiary species remain, which either appear definitely acritarchs or whose morphology is not at present sufficiently well known for any

reattribution to be made. These are, for the time being, left in the genus *Baltisphaeridium*; they are as follows:

Baltisphaeridium armatum (Deflandre, 1937) Downie & Sarjeant 1963. Upper Cretaceous; France.

B. asteroideum (Maslov 1956) Downie & Sarjeant 1963. Upper Cretaceous; Cauacusus, U.S.S.R.

B. claviculorum (Deflandre 1938) Downie & Sarjeant 1963. Upper Jurassic; France.

B. clavispinulosum Churchill & Sarjeant 1963. Quaternary; Australia.

B. densicomatum (Maier 1959) Gerlach 1961. Oligocene; Germany.

B. denticulatum (Courteville *in* Deflandre 1946) Downie & Sarjeant 1963. Upper Cretaceous; France.

B.? difforme (Pritchard 1841) Downie & Sarjeant 1963. Upper Cretaceous; England.

B. downiei Sarjeant 1960*a*, Upper Jurassic; England.

B. echiniplax Churchill & Sarjeant 1963. Quaternary; Australia.

B. fimbriatum (White 1842) Sarjeant 1959. Upper Cretaceous; England.

B. gilsonii (Kufferath 1950) Downie & Sarjeant 1963. Quaternary; Belgium.

B. horridum (Deflandre 1937) Downie & Sarjeant 1963. Upper Cretaceous; France.

B. huguonioti (Valensi 1955) Downie & Sarjeant 1963. Cretaceous; France.

B. intermedium (O. Wetzel 1933) Downie & Sarjeant 1963. Upper Cretaceous; Baltic.

B. longofilum (Maier 1959) Downie & Sarjeant 1963. Oligocene; Germany.

B. malleoferum (White 1842) Downie & Sarjeant 1963. Upper Cretaceous; England.

B. mariannae (Philippot 1949) Downie & Sarjeant 1963. Upper Cretaceous; France.

B. panniforme Gerlach 1961. Oligocene; Germany.

B. pattei (Valensi 1948) Sarjeant 1960*a*. Middle Jurassic; France.

B. paucifurcatum (Cookson & Eisenack 1961*b*) Downie & Sarjeant 1964. Eocene; Australia.

B. pectiniforme Gerlach 1961. Oligocene; Germany.

B. plicatum (Maier 1959) Downie & Sarjeant 1963. Oligocene; Germany.

B. (?) *polyceratum* Takahashi 1964. Oligocene; Japan.

B. polyozon Brosius 1963. Oligocene; Germany.

B. quaternarium Churchill & Sarjeant 1963. Quaternary; Australia.

B. saturnium (Maier 1959) Downie & Sarjeant 1963. Miocene ; Germany.

B. seminudum (W. Wetzel 1952) Downie & Sarjeant 1963. Paleocene (Danian) ; Baltic.

B. spiculatum (White 1844) Downie & Sarjeant 1963. Upper Cretaceous ; England.

B. stimuliferum (Deflandre 1938) Sarjeant 1960*c*. Upper Jurassic ; France.

B. sylheti (Baksi 1963) Downie & Sarjeant 1964. Eocene ; Assam, India.

B. telmaticum Churchill & Sarjeant 1963. Quaternary ; Australia.

B. tinglewoodense Churchill & Sarjeant 1963. Quaternary, Australia.

B. varispinosum Sarjeant 1959. Middle Jurassic ; England.

B. whitei (Deflandre & Courteville 1939) Downie & Sarjeant 1963. Upper Cretaceous ; France.

It is apparent, from illustrations and descriptions, that the bulk of these species will be demonstrated in the future also to be the cysts of dinoflagellates ; acritarchs appear relatively infrequent after the Palaeozoic. Five of the species listed are freshwater forms from the Australian Quaternary ; a restudy of their taxonomy is in progress.

VIII. THE GENUS *HYSTRICHOKOLPOMA*

By G. L. WILLIAMS & C. DOWNIE

INTRODUCTION

The appearance of *Hystrichokolpoma* makes it one of the most striking of the Tertiary dinoflagellate cysts. It occurs in small numbers throughout the London Clay where its excellent preservation enables the tabulation to be determined completely in many circumstances. Two previously described and one new species are recorded.

Genus ***HYSTRICHOKOLPOMA*** Klumpp 1953 : 388

EMENDED DIAGNOSIS. Chorate cysts bearing two types of intratabular processes, large types with expanded bases, and slender ones. Large processes have proximally a quadrate cross section reflecting plate outline. Slender processes delimiting well marked cingular and sulcal zone. Cingulum helicoid. Reflected tabulation of 4′, 6″, 6g, 5‴, 1p, 1⁗. Archeopyle apical tetratabular.

TYPE SPECIES. *Hystrichokolpoma cinctum* Klumpp 1953. Eocene ; Germany.

DISCUSSION. *Hystrichokolpoma* is a genus with a spherical to ellipsoidal central body possessing intratabular processes, radial symmetry and an apical archeopyle. Each large process almost completely occupies a single plate proximally assuming the outline of the plate leaving only a narrow border all round. Distally these processes taper and may be open or closed. They are restricted to the apical, precingular, postcingular, antapical and commonly anterior sulcal plates. The antapical plate is easily recognizable, having a longer process than the others. The slender processes are restricted to the cingular and sulcal zones. The number of equatorial processes per plate is constant in an individual but can vary within the species as now defined (personal communication from Dr. W. R. Evitt). The apical plates are rarely found in position. Breakage along sutures readily occurs when attempting to mount specimens of *Hystrichokolpoma*. Process variation in structure and number is considerable and needs careful study.

Hystrichokolpoma eisenacki sp. nov.

Pl. 17, figs. 1–3 ; Text-fig. 46

1954. *Hystrichokolpoma cinctum* Klumpp ; Eisenack : 64, pl. 10, figs. 11–14.

DERIVATION OF NAME. After Prof. Alfred Eisenack, pioneer worker on fossil dinoflagellates.

DIAGNOSIS. Ellipsoidal central body with wall composed of two closely appressed layers—the smooth or granular endophragm and the thinner smooth periphragm. Endophragm continuing uninterrupted beneath processes formed from periphragm.

Processes of two types, large ones with quadrate bases, cylindrical or tapering with open ends, and small slender processes, with ends open or closed. Antapical process much longer than others. Tabulation typical for genus. Number of slender processes on each cingular plate limited to two. Cingulum helicoidal. Anterior sulcal process considerably larger than other sulcals.

HOLOTYPE. B.M.(N.H.) slide V.51958(1), London Clay; Sheppey, Kent, sample Sh. 3.

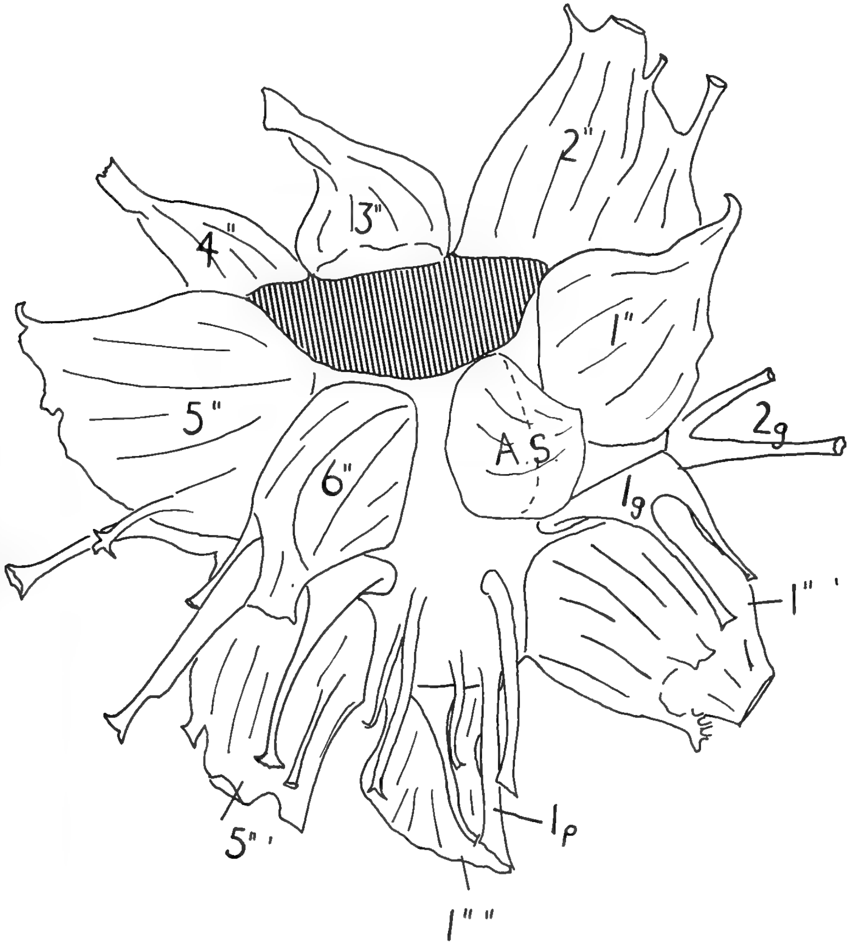


FIG. 46. *Hystrichokolpoma eisenacki* sp. nov. Ventral view of holotype showing the Tabulation. The archaeopyle is shaded.

Dimensions. Holotype : diameter of central body 47 by 52μ. Broad processes, length up to 30μ, breadth up to 27μ. Length of slender processes up to 22μ. Range of dimensions observed ; diameter of central body 40–57μ. Length of broad processes 20–30μ. Antapical process up to 47μ. Width of broad processes 12–27μ. Length of slender processes 13–20μ. Width of slender processes 0·5–4μ. Number of specimens measured, 4.

Description. *H. eisenacki* is characterized by the broad processes which taper distally to a restricted opening with entire or serrate margin. Frequently branching off from the large processes are small erect tubules with an open serrate distal margin ; commonly there are three or four on each process. The equatorial processes are simple or branched, slender with slightly expanded distal openings. The four apical plates are rarely present ; the archaeopyle has a broad sulcal notch. In the precingular series of plates, plate 6″ and its attendant process are considerably smaller than the other five plates and processes, being comparable in size to the anterior sulcal plate and process. In the postcingular series, plate 1‴ and its process are the smallest of the series, the other four plates and processes approaching the precingulars in size. The longest process, which tapers before expanding distally, marks the position of the single antapical plate. This process is usually closed and unbranched. There are six sulcal processes, one very large anterior process and five very slender open or bifid or acuminate processes lying between plates 1‴ and 5‴. The single posterior intercalary process is little different in size and structure to the slender sulcal processes and occupies a position between 1‴ and 1⁗. The apical processes are usually simple, occasionally branched, tapering and open distally.

Occurrence. London Clay, Whitecliff and Enborne and the Oligocene of Samland, East Prussia (Eisenack 1954).

Remarks. The authors are indebted to Dr. W. R. Evitt of Stanford University for placing at their disposal camera lucida drawings of the holotype of *Hystrichokolpoma cinctum* Klumpp (1953) and the originals of *H. cinctum* Klumpp of Eisenack (1954) ; they are quite different species. The drawings show that *H. eisenacki* and Eisenack's (1954) specimens of *H. cinctum* have similar tabulation and differ only in that the former has tubular branches, and not pointed spines, arising from the broad processes. Both are, however, included within the same species here named *H. eisenacki*. *H. eisenacki* differs from *H. cinctum* Klumpp (1953) in the dorsal terminations of the broad processes which are more commonly branched, the smaller number of cingular processes and the possession of a large anterior sulcal process and plate.

Hystrichokolpoma eisenacki var. ***turgidum*** nov.

Pl. 17, fig. 5

Derivation of name. Latin, *turgidus*, inflated, swollen, distended.

Diagnosis. Central body ovoidal slightly granular, bearing processes of two types, broad sub-conical or bulbose, with wide or restricted distal opening and slender, simple or bifurcate processes open or closed distally.

HOLOTYPE. B.M.(N.H.) slide V.51959(1). London Clay ; Enborne, sample E 11.

DIMENSIONS. Holotype : diameter of central body 40–41μ. Length of broad processes up to 21μ. Length of slender processes up to 24μ. Range of dimensions observed : diameter of central body 44–56μ. Length of broad processes 20–30μ, width of broad processes 8–26μ. Length of slender processes 16–28μ, width of slender processes usually 1–3μ. Number of specimens measured, 3.

DESCRIPTION. The broad processes of *H. eisenacki* var. *turgidum* may be subconical and widely open distally or bulbose with a restricted opening that has a serrate, commonly recurved, margin. Branching similar to that in *H. eisenacki* can occur, but there are rarely more than one or two branches. The longer tapering antapical process sometimes has very small tubules arising laterally and appears minutely open distally. The broad processes give rise to a characteristic trapezoid outline where they join the central body. The slender equatorial processes are variable in number, generally being restricted to two per plate, with infrequently three occurring. They are open with a digitate or serrate distal margin or they are bifurcate. Often they arise in pairs, being united proximally for as much as $\frac{1}{3}$ of their length. The tabulation is as in *H. eisenacki* with a reduced sixth precingular plate and a large anterior sulcal plate.

OCCURRENCE. London Clay ; Enborne and Sheppey.

REMARKS. *H. eisenacki* var. *turgidum* differs from *H. cinctum* in the number of cingular processes and the presence of a large anterior sulcal plate and process, and from the typical form of *H. eisenacki* in the usual presence of broad processes that have three or four branches distally.

Hystrichokolpoma unispinum sp. nov.

Pl. 17, figs. 6, 7

DERIVATION OF NAME. Latin, *uni*—one ; *spina*, spine.

DIAGNOSIS. Central body sub-spherical with thin smooth endophragm, continuous beneath processes, and thin smooth periphragm. Processes formed from periphragm and of two types, broad tapering lagenate, and buccinate more slender processes. Reflected tabulation of 4′, 6″, 6g, 5‴, 1p, 1⁗ and at least 5s. Each cingular plate possessing only one process.

HOLOTYPE. B.M.(N.H.) slide V.51961(1), London Clay ; Whitecliff, sample WC 8.

DIMENSIONS. Holotype : diameter of central body 39 by 43μ. Length of broad processes up to 29μ, width up to 21μ. Slender processes, length up to 26μ, width up to 5μ. Range of dimensions observed : diameter of central body 39–51μ. Length of broad processes 21–29μ, breadth up to 21μ. Equatorial processes, length 18–26μ, breadth up to 5μ. Number of specimens measured, 3.

DESCRIPTION. The tabulation of *H. unispinum* is well shown in two specimens from the London Clay. There are four apical plates, 1′ being smaller than the other three. The apical processes are tapering, open distally with a serrate or undulose margin. Five of the precingular plates and processes are equal in size, the other, plate 6″, is smaller, more closely approaching the anterior sulcal plate. The equatorial plates each possess one process. The postcingulars are as in *H. eisenacki*, with plate 1‴ being reduced compared to the other four. The process of the posterior intercalary plate is small and the antapical plate is marked by a longer than average process.

The broad processes all appear open distally and may have small tubular branches. The equatorial processes are broader than in other species of *Hystrichokolpoma* and are tubiform or buccinate with serrate or undulose distal margins. A few have perforations in the wall, irregular in position. The processes may occasionally be branched. The posterior sulcal processes are slender and short with digitate endings which may be open or closed.

OCCURRENCE. London Clay ; Whitecliff and Enborne.

REMARKS. The presence of one process only on each cingular plate readily distinguishes *H. unispinum* from other species of *Hystrichokolpoma*.

Hystrichokolpoma rigaudae Deflandre & Cookson

Pl. 17, fig. 4

1954. *Hystrichokolpoma rigaudae* Deflandre & Cookson, text-fig. 15 (*n.n.*).
1955. *Hystrichokolpoma rigaudae* Deflandre & Cookson : 279, pl. 6, figs. 6–10 ; text-fig. 42.
1959. *Hystrichokolpoma rigaudae* Deflandre & Cookson ; Maier : 311, pl. 31, fig. 2.
1961. *Hystrichokolpoma rigaudae* Deflandre & Cookson ; Gerlach : 183, pl. 27, figs. 8, 9.
1962. *Hystrichokolpoma rigaudae* Deflandre & Cookson ; Rossignol : 134.
1963. *Hystrichocolpoma rigaudae* Deflandre & Cookson ; Brosius : 43, pl. 2, fig. 6.
1964. *Hystrichokolpoma rigaudae* Deflandre & Cookson ; Rossignol : 89, pl. 2, fig. 5, pl. 3, fig. 8.

DISCUSSION. Specimens of *H. rigaudae* from the London Clay possess a tabulation of 6″, 6c, 5‴, 1p, 1⁗ and 6a. Plates 6″ and 1‴ and their attendant processes are reduced whilst the anterior sulcal plate is the largest of the six. A few of the broad processes and some of the girdle ones are open distally. There seems to be a degree of variability in the number of cingular processes, some plates having only one ; generally however there are two processes on each cingular plate.

DIMENSIONS. Observed range in London Clay : diameter of central body 35–48μ. Length of broad processes up to 31μ. Length of antapical process up to 39μ. Number of specimens measured, 3.

OCCURRENCE. London Clay ; Whitecliff, Enborne and Sheppey. *H. rigaudae* has also been recorded from the Eocene and Miocene (or older) of Australia (Deflandre & Cookson 1954, 1955), the Middle Oligocene–Middle Miocene (Gerlach 1961), the Upper Oligocene (Brosuis 1963) and the Middle Miocene of Germany (Maier 1959) and the Pleistocene of Israel (Rossignol 1962, 1964).

OTHER SPECIES

Re-examination of *Baltisphaeridium ferox* (Deflandre 1937*a*) Downie & Sarjeant 1963, *B. tridactylites* (Valensi 1955), Downie & Sarjeant, 1963 and *Hystrichosphaeridium clavigerum* Deflandre 1937*a*, by Mr. R. J. Davey and Prof. Deflandre, has determined that these species should be transferred to the genus *Hystrichokolpoma*.

The remaining species attributed to this genus are *H. sequanapartus*, Deflandre & Deflandre-Rigaud 1958, and *H. poculum* Maier 1959. A single specimen of a form very like the former was found in the London Clay.

IX. *WETZELIELLA* FROM THE LONDON CLAY

By G. L. WILLIAMS & C. DOWNIE

INTRODUCTION

The characteristic Lower Tertiary genus *Wetzeliella* is among the commonest of the London Clay dinoflagellates. The excellent state of preservation has enabled its tabulation to be determined in many instances and its resemblance to the living genus *Peridinium* is established beyond doubt. Several new forms have been discovered and it is now possible to give a fuller description of some species already named.

Genus ***WETZELIELLA*** Eisenack 1938 : 186

Type species. *Wetzeliella articulata* Eisenack 1938.

Emended diagnosis. Body with distinct pericoel and endocoel. Periphragm having a distinctive outline, varying from oval to pentagonal and generally prolonged into an apical horn, two lateral horns and one or two antapical horns. Periphragm may or may not bear intratabular processes. Processes (when present) open proximally, open or closed distally and frequently arranged in process complexes. Endophragm circular to ovoid in outline, in cross section biconvex and separated, by pericoel of variable size from periphragm. Reflected tabulation of 4′, 3a, 7″, 5‴, 2⁗, 3–4s, ?c not always evident. Cingulum slightly laevo-rotatory, running round maximum width of periphragm. Sulcus wider and longer on hypotract than epitract. Archaeopyle usually present in periphragm and resulting from loss of plate 2a. Endophragm usually with archaeopyle in analogous position.

Discussion. *Wetzeliella* is related to the living genus *Peridinium*, since it possesses identical tabulation and the same type of archaeopyle. It is distinguishable from *Peridinium* by the presence of usually well developed lateral horns, and in most cases by the numerous processes on the pericoel and the easily recognizable endocoel. Eisenack's (1964) placing of *Wetzeliella* and *Deflandrea* in a separate sub-order from *Peridinium* appears to be an artificial classification which disregards the evidence of tabulation. *Dracodinium* Gocht, 1955, is no longer recognized as a separate genus, since all stages of transition from *Dracodinium solidum*, the sole species of the genus, to *Wetzeliella similis* (Eisenack) occur in the London Clay. *D. solidum* (pars) is therefore placed in the genus *Wetzeliella*. Gocht's statement that the position of the slip hole (archaeopyle) is variable, prevents the complete incorporation of *Dracodinium solidum* in *Wetzeliella*. Two sub-genera of *Wetzeliella* are recognized, *Wetzeliella* (*Wetzeliella*) Eisenack and *Wetzeliella* (*Rhombodinium*) (Gocht) Alberti, 1961.

The tabulation, which in many species is hard to determine, has been worked out for *W. articulata*, *W. clathrata* Eisenack, *W. coleothrypta* sp. nov., *W. reticulata* sp. nov. *W. tenuivirgula* sp. nov., *W. homomorpha* Deflandre & Cookson 1955, *W. condylos* sp. nov., and *W. similis* Eisenack 1954. In the sub-genus *Wetzeliella* (*Rhombodinium*) usually the only guide to tabulation is the archaeopyle.

Sub-genus *Wetzelliella* (*Wetzelliella*) Eisenack 1938.

DIAGNOSIS. A sub-genus of the genus *Wetzeliella*, possessing numerous processes developed from the periphragm. Processes showing only moderate variation in length and may be united distally. Processes intratabular, forming simulate complexes, or haphazardly distributed on plate.

TYPE SPECIES. *Wetzeliella* (*Wetzeliella*) *articulata* Eisenack 1938.

Wetzeliella* (*Wetzeliella*) *articulata Eisenack

Pl. 18, figs. 1–4

1935. *Peridinium* sp., O. Wetzel : 168, pl. 2, fig. 1.
1938. *Wetzeliella articulata* Eisenack : 186, text-fig. 4.
1950. *Wetzeliella articulata* Eisenack ; Reissinger : 119, pl. 19, fig. 6.
1952. *Wetzeliella articulata* Eisenack ; Gocht : 314, pl. 2, figs. 38, 39.
1952. *Wetzeliella articulata* Eisenack ; Deflandre, text-fig. 89.
1953. *Wetzeliella articulata* Eisenack ; Klumpp : 393, pl. 19. figs. 1–5.
1954. *Wetzeliella articulata* Eisenack ; Eisenack : 55, pl. 7, figs. 1–11 ; pl. 8, figs. 14–16.
1956. *Wetzeliella articulata* Eisenack ; Cookson : 185, pl. 2, fig. 6.
1959*a*. *Wetzeliella articulata* Eisenack ; Eisenack, pl. 3, fig. 7.
1961. *Wetzeliella articulata* Eisenack ; Evitt : 397, pl. 8, figs. 3, 5, 6.
1961. *Wetzeliella articulata* Eisenack ; Gerlach : 152, pl. 25, fig. 2.

DISCUSSION. *W.* (*W*) *articulata* is of widespread occurrence in the London Clay of Enborne and Sheppey but is uncommon at Whitecliff. The London Clay specimens do not vary from the type material. The tabulation has beeen worked out in a few individuals, from the alignment of some of the intratabular processes in simulate complexes. These are four apicals, three anterior intercalaries (of which plates 1a and 3a are elongate) ; seven precingulars (with plates 2″ and 6″ elongate) ; 5 post-cingulars (all well developed plates) ; two antapicals of approximately equal size and three sulcals, with the posterior sulcal plate the largest. That the endophragm is subdivided into plates of similar orientation is suggested by the regularly orthogonal outline of the inner archaeopyle.

Of the two antapical horns always present in *W.* (*W*) *articulata* the longer invariably lies to the right of the mid-ventral line, (for definition see Evitt 1963). The processes forming the simulate complexes lie just in from the plate boundaries. A few of the London Clay specimens have granular processes. Beautifully formed crystals of pyrite are found in the horns of some specimens but only rarely in the endocoel.

Specimens intermediate to *Wetzeliella symmetrica* Weiler (1956) from the Oligocene of Germany, are not uncommon in the London Clay. These possess a reduced left antapical horn and/or an elongate apical horn, a length/breadth ratio of approximately 1 to 1 and are probably synonymous with *W.* cf. *symmetrica* (Weiler) Maier (1959). Gerlach (1961) in a discussion of *W. symmetrica symmetrica* Weiler, mentions the occurrence of specimens with a second antapical horn. Unfortunately she did not figure any such types.

Other individuals having a reduced apical horn and sometimes also a poorly developed left antapical horn are intermediate to *W. similis* Eisenack. These are of less frequent occurrence than the previously described forms.

The forms recorded by Pastiels (1948) as *Hystrichosphaeridium articulatum* and transferred to *W. articulata* by Eisenack (1954), are not in fact representatives of this latter species. The diagnostic characteristics of *W. articulata* are the possession of a well developed apical horn and two well developed antapical horns, usually unequal in size. Pastiels' forms do not have this well developed second antapical horn and are transferred to *W.* (*W*) *symmetrica* var. *lobisca* (see p. 196).

Dimensions. Observed range in London Clay: outer shell length 111–162μ, breadth 64–105μ. Number of specimens measured, 28.

Occurrence. Eocene, London Clay; Whitecliff, Studland, Sheppey and Enborne. *W. articulata* has been recorded in Europe from the Lower Eocene to the Middle Miocene.

Wetzeliella* (*Wetzeliella*) *articulata var. ***conopia*** nov.

Pl. 18, fig. 5

Derivation of name. Greek, *konopos*—gnat.

Holotype. B.M.(N.H.) slide V.51962. London Clay; Sheppey, Kent, sample SL.4.

Dimensions. Holotype: outer shell length 132μ, breadth 126μ, Capsule length 88μ. Observed range: outer shell, length 120–156μ. Capsule, length 88–105μ, breadth 83–92μ. Number of specimens measured, 4.

Description. A variety of *W.* (*W*). *articulata* having processes that distally may give rise to long aculei, often interconnected with aculei of adjacent processes. This is an intermediate form to *W.* (*W*). *leptavirgula* sp. nov. It has been found in the London Clay only at Sheppey.

Wetzeliella* (*Wetzeliella*) *clathrata Eisenack

Pl. 18, fig. 6

1938. *Wetzeliella clathrata* Eisenack: 187, text-fig. 5.
1954. *Wetzeliella clathrata* Eisenack; Eisenack: 57, pl. 7, figs. 12–14; text-fig. 2.
1961. *Wetzeliella clathrata* Eisenack; Gerlach: 153, pl. 25, fig. 6.
1961. *Wetzeliella clathrata* Eisenack; Evitt: 397, pl. 1, fig. 19.

Discussion. A single specimen from the London Clay is attributed to *W.* (*W*). *clathrata*. Many individuals that on initial examination appear to belong to *W. clathrata* are really examples of *W.* (*W*). *coleothrypta*. *W. clathrata* is a distinctive species whose processes are aligned in rows, immediately within the boundary of a plate, forming simulate complexes. Adjacent processes are united distally by perforate membranes restricted in width to a few microns; these are the "lists" of Eisenack. Tabulation is as in *W. articulata* and the reduced antapical horn lies to the left of the mid-ventral line.

Wetzeliella* (*Wetzeliella*) *coleothrypta sp. nov.

Pl. 18, figs. 8, 9 ; Text-fig. 47

DERIVATION OF NAME. Greek, *koleos*, scabbard, sheath ; *thrypto*, break.

DIAGNOSIS. Thin walled periphragm characteristic pentagonal outline with each angle produced into horns, one apical, two lateral and two antapical ; left antapical horn generally reduced. Pericoel totally enclosing endophragm. Processes arising from periphragm, hollow, connecting with pericoel. Distally processes of individual simulate complex united by finely perforate membrane assuming outline of underlying plate and extending over that plate as a replica of it. Processes commonly absent from pre- and postcingular plates on side lying nearest to cingulum. Reflected tabulation of 4′, 3a, 7″, 5c, 5‴, 2″, 3–4s.

HOLOTYPE. B.M.(N.H.) slide V.51753(3). London Clay ; Sheppey, Kent, sample Sh.4.

DIMENSIONS. Holotype : periphragm length 122μ ; breadth 110μ. Capsule length 69μ ; breadth 61·5μ. Observed range : outer shell length 112·5–157μ ; breadth 102·5–142μ. Capsule length 66–106μ ; breadth 67–97μ. Processes up to 15μ long. Number of specimens measured, 6.

DESCRIPTION. The periphragm of *W. coleothrypta* has an outline approaching *W. similis* on the one hand and *W. articulata* on the other. The right antapical horn is invariably longer than the left, which is often represented by a small protuberance. The apical horn has a pointed apex ; the lateral horns are indented distally due to the transverse cingulum crossing from the dorsal to the ventral surface at these two places. The slender, simple, or occasionally branched processes are intratabular,

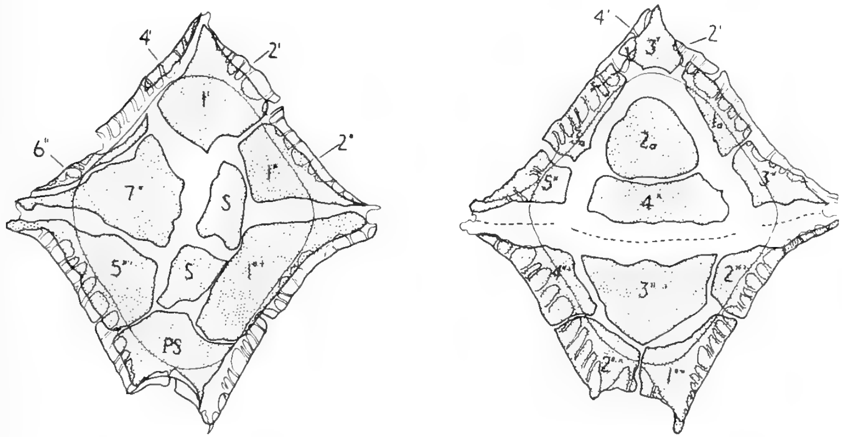


FIG. 47. *Wetzeliella* (*Wetzeliella*) *coleothrypta* sp. nov. Left, tabulation of ventral (upper) surface of holotype ; right, tabulation of dorsal (lower) surface. S, sulcal plates ; PS, posterior sulcal plate ; stippled areas show where processes are united distally by a membrane.

arising from just within the plate boundary and usually forming a simulate complex on each plate. The processes of each complex are united distally by a membrane which is finely perforate and which assumes the outline and area of the underlying plate. The general rule that the longer the processes, the further away they are from the horns, is found to be true for this species.

The plates, interpreted from the simulate complexes, show considerable variation in size. Of the apicals, plate 1′ is by far the largest and has a trapezoid outline : plates 2′ and 4′ are lateral in position and are narrow, being represented by a single row of processes ; whilst the dorsal plate 3′ is intermediate in size between 1′ and 4′. The anterior intercalary plates likewise vary in size and are dorsal in position. Plates 1a and 3a are elongate, narrowing apically, whereas plate 2a, the loss of which forms the archaeopyle, is trapezoid, with processes absent from its equatorial boundary. The seven precingulars show extreme variation. Plates 1″ and 7″ are of comparable size with an almost triangular outline. Plates 2″ and 6″ are extremely narrow and are represented by a single row of processes running along the lateral margin. On the dorsal surface, the three plates 3″, 4″, and 5″ are wider than the others and do not extend as far towards the apex, being restricted because of the anterior intercalaries. Plate 4″ is the widest of the precingular series.

The circular cingulum comprises five plates, three on the dorsal surface, two on the ventral. Each plate has a single row of processes that are united distally as in *W. clathrata*. Of the postcingulars, plates 1‴ and 5‴ on the ventral surface are of comparable size and shape (see Fig. 47), whilst plates 2‴ and 4‴ are smaller though of not dissimilar outline. The widest of the postcingulars is plate 3‴, which usually has no processes on the side adjacent to the transverse cingulum. This is also frequently true of most of the pre- and postcingular plates. The two antapical plates are dorsally situated. The sulcus is considerably expanded on the hypotract and extends to the distal extremities of the antapical horns. There can be three or four sulcal plates, of which the most posterior is the largest and has a rhomboidal shape. Only one sulcal plate is present on the epitract. The tabulation is always clearly shown and easily decipherable.

The width of the pericoel has no bearing on the thickness of the capsule wall, in this or any other species of *Wetzeliella*. Thin walled capsules often lie at a considerable distance from the periphragm. Evitt's (1961*c*) hypothesis that the greater the distance of the capsule from the enclosing periphragm, the thicker the endophragm, must therefore be applied with caution. The capsule of *W. coleothrypta* may be slightly granular ; it possesses an archaeopyle which is in line with that of the periphragm and appears to be intercalary. The operculum of the archeopyle is often found lying within the capsule.

Remarks. Of the described species of *Wetzeliella*, only *W. clathrata* has processes united distally. However, whereas in *W. clathrata* the processes are united so as to give lists or bars of restricted width, in *W. colethrypta*, the membrane assumes the outline of the plate and passes completely over it, forming an outer umbrella. The two species can therefore be easily distinguished.

Wetzeliella (*Wetzeliella*) *reticulata* sp. nov.

Pl. 19, figs. 3, 6 ; Text-fig. 48

DERIVATION OF NAME. Latin, *reticulatus*, netted, net-like.

DIAGNOSIS. Periphragm with distinctive pentagonal outline, produced into horns at each angle ; one apical, two lateral and two antapical horns. Right antapical always larger than left antapical horn. Periphragm totally enclosing ovoidal capsule. Surface of periphragm bearing intratabular processes, usually restricted to simulate complexes ; processes lying immediately within boundaries of plates. Processes diversely united within each complex by series of trabeculae, giving a reticulum extending over plate and assuming plate outline. Processes of adjacent plates not unified. Reflected tabulation 4′, 3a, 7″, 5c, 5‴, 2⁗, 3 or 4s. Archaeopyle present.

HOLOTYPE. B.M.(N.H.) slide V.51752(6). London Clay ; Sheppey, Kent, sample 2.

DIMENSIONS. Holotype : periphragm length 146μ, breadth 162·5μ, capsule length 106μ, breadth 110μ. Observed range : outer shell length 146–167μ, breadth 150–162·5μ. Capsule length 103–106μ, breadth 95–110μ. Number of specimens measured, 2.

DESCRIPTION. The shape and size of the plates of the periphragm of *W. reticulata* agree with those of *W. coleothrypta* (see previous description). The hollow, closed, cylindrical processes, in connection with the pericoel cavity are distally divided into numerous secae which ramify and are united by means of trabeculae with secae from processes of the same plate. The boundary of the reticulum thus formed is extremely regular, unconnected spines branching off only infrequently. Each reticulum mirrors the shape of the plate it overlies and is only slightly smaller. The trabeculae of the reticulum are taeniate.

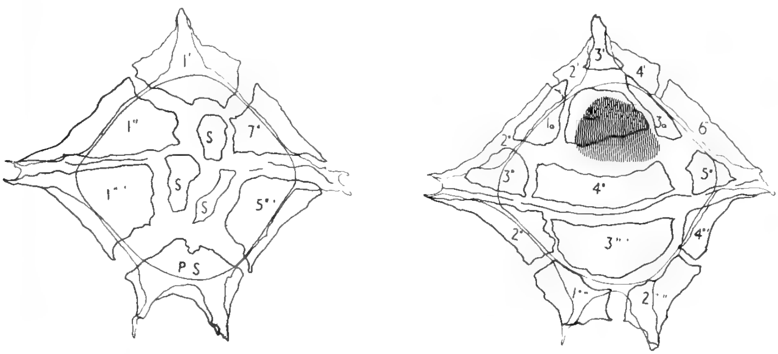


FIG. 48. *Wetzeliella* (*Wetzeliella*) *reticulata* sp. nov. Left, tabulation of the ventral (lower) surface of holotype ; right, tabulation of the dorsal (upper) surface. Stippling denotes area of simulate process complexes. The archaeopyle in the endophragm resulting from loss of plate 2a is shaded.

Processes can arise from any point on a plate within the simulate complex, sometimes even forming secondary rows, further strengthening the reticulum.

The capsule is large, almost filling the pericoel apart from the horns. It has a thin slightly granular wall.

OCCURRENCE. Eocene, London Clay ; Sheppey.

REMARKS. *W. reticulata* has an outline closely approaching *W. articulata* which can occasionally have processes that are united distally, but never in the form of a reticulum reflecting each individual plate constituting the pericoel. *W. reticulata* differs from *W. coleothrypta* in the distal structure of the processes and in having two well developed antapical horns.

Wetzeliella* (*Wetzeliella*) *tenuivirgula sp. nov.

Pl. 19, figs. 2, 4 ; Text-fig. 49

DERIVATION OF NAME. Latin, *tenuis*, thinned ; *virgula*, small twig—referring to the processes.

DIAGNOSIS. Periphragm outline pentagonal to ovoidal, with each angle produced into a well developed tapering horn—one apical, two lateral and one or two antapical. Right antapical horn always the longer. Periphragm flattened in cross section, save medially where it encloses the ovoidal capsule. Hollow, slender or branched processes arising from periphragm and arranged in simulate complexes or occurring haphazardly within complexes. Processes terminating distally in elongate, solid secae, sometimes united to secae of adjacent processes ; giving rise to interconnections between processes on opposite sides of plate or remaining unconnected. Tabulation typical of genus, with three sulcal plates. Archaeopyle usually formed.

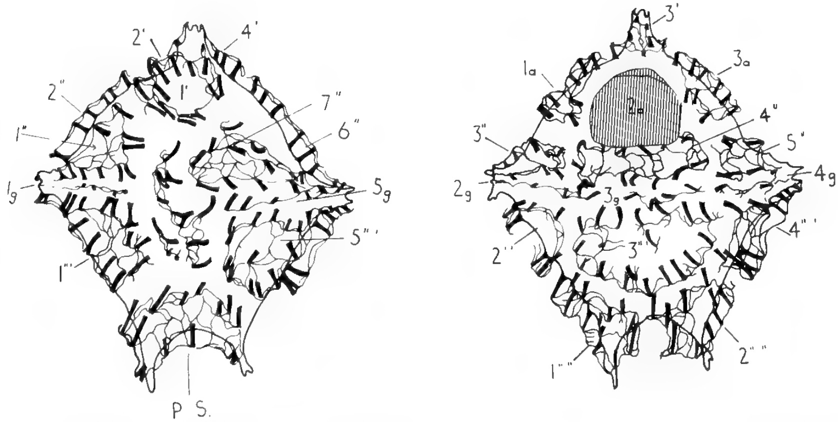


FIG. 49. *Wetzeliella* (*Wetzeliella*) *tenuivirgula* sp. nov. Left, tabulation of ventral (lower) surface of holotype ; right, tabulation of dorsal (upper) surface. Shading indicates archaeopyle.

HOLOTYPE. B.M.(N.H.) slide V.51964(2). London Clay ; Sheppey, Kent, sample 2.

DIMENSIONS. Periphragm, length 125–175μ ; breadth 120–158μ. Capsule, length, 72–113μ ; breadth 70–104μ. Number of specimens measured, 9.

DESCRIPTION. *W. tenuivirgula* commonly has an outline similar to that of *W. articulata*, with two well-developed antapical horns, although the left is absent in some individuals. The apical and antapical horns are acuminate distally ; the lateral horns are indented, denoting the position of a cingulum. The processes tend to be graded, being longest furthest away from the horns.

OCCURRENCE. Eocene, London Clay ; Sheppey and Enborne.

In some specimens the majority of the processes are regularly arranged just within the plate boundary and form a simulate complex ; they may also arise nearer the plate centre. The secae, besides uniting adjacent processes, often extend across the plate, thus giving rise to a very loosely knit reticulum, totally different, in appearance to that found in *W. reticulata*. Unconnected acuminate spines, up to 2–3μ in length, often arise from the interconnecting secae or trabeculae. The trabeculae may be granular or smooth ; the secae are usually extremely fine and regular. Processes of adjacent plates are not united. The pre- or postcingular plates may or may not have processes on the side nearest the cingulum. The capsule almost fills the pericoel, apart from the horns, and has a slightly granular wall.

W. tenuivirgula differs from *W. reticulata* in the nature of the secae ; in the latter species these are short and complexly anastomosing and are rarely unconnected.

Wetzeliella **(*Wetzeliella*)** ***tenuivirgula*** var. ***crassoramosa*** nov.

Pl. 19, figs. 1, 5, 7 ; Text-fig. 50

DERIVATION OF NAME. Latin, *crassus*, thick, stout ; *ramosus*, branching ; hence thick-branched.

HOLOTYPE. B.M.(N.H.) slide V.51954(2). London Clay ; Whitecliff, sample WC4.

DIMENSIONS. Holotype : outer shell length 125μ ; breadth 122μ. Capsule—length 80μ ; breadth 71μ. Observed range : outer shell length 125–182μ ; breadth 122–160μ. Capsule, length 80–144μ ; breadth 71–103μ. Number of specimens measured, 8.

DESCRIPTION. This differs from the typical *W. tenuivirgula* in the nature of the distal branching of the processes ; the secae and trabeculae are much wider and taeniate, the reticulum being much stronger as a result. The processes forming the simulate complexes are often united by particularly wide taeniate secae (or bars) up to 3μ in width. Frequently there are simple unconnected spines with blunt or bulbous terminations branching off from the bars and trabeculae. In outline, the outer shell lies between that of *W. articulata* and *W. symmetrica*, individuals with an outline approaching the latter species predominating.

OCCURRENCE. Eocene, London Clay ; Whitecliff.

REMARKS. *W. tenuavirgula* var. *crassoramosa* does not merit raising to specific level, on account of the frequent occurrence of forms transitional to *W. tenuovirgula*. The extreme development of the secae (more correctly termed bars at this stage of development) however is very distinctive.

Wetzeliella* (*Wetzeliella*) *homomorpha Deflandre & Cookson

1948. *Hystrichosphaeridium geometricum* Pastiels (pars) : 41, pl. 4, figs. 3, 5, 6, 7, 9, 10.
1955. *Wetzeliella homomorpha* Deflandre & Cookson : 254, pl. 5, fig. 7 ; text-fig. 19.

DISCUSSION. The species *W. homomorpha* is restricted to forms having a periphragm with rhomboidal, ovoidal or sub-circular outline and which lacks well developed horns. The processes tend to be concentrated on the ambitus and are generally closed distally. The archaeopyle is intercalary. Deflandre & Cookson (1955) stated that none of the Australian examples contained the internal " cyst " characteristic of *Wetzeliella*. Their " cyst " formed by the endophragm is in fact present in the forms from the London Clay, but is easily overlooked, since it lies close to and follows the outline of the pericoel. *W. homomorpha* is therefore a species of *Wetzeliella* in which the periphragm and endophragm are almost in contact throughout.

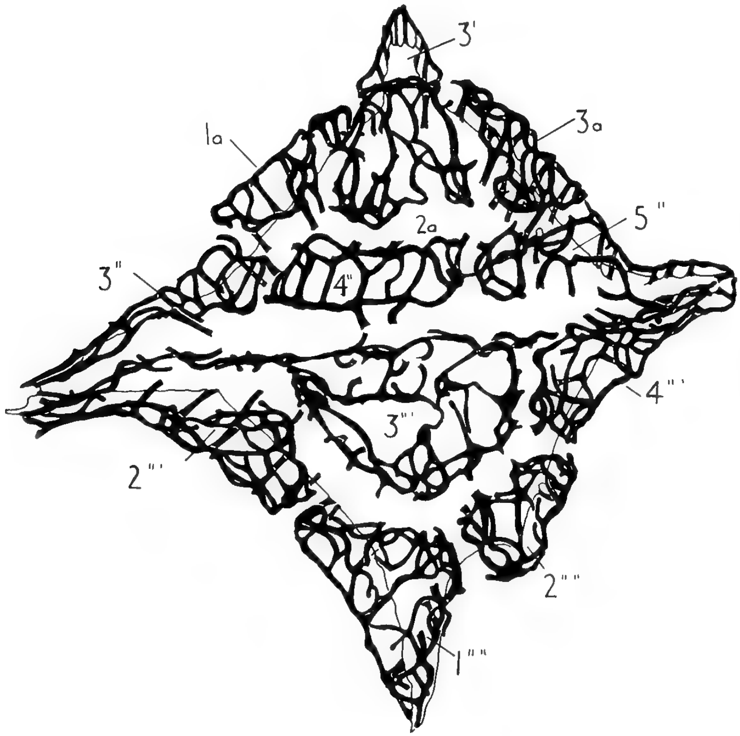


FIG. 50. *Wetzeliella* (*Wetzeliella*) *tenuivirgula* var. *crassoramosa* nov. Tabulation of dorsal surface, showing simulate complexes.

The processes of specimens of *W. homomorpha* from the London Clay are variable, simple or branched, single or in linear complexes, distally bifid, blunt or acuminate or with restricted opening. When open the processes have an entire margin. It is impossible to distinguish varieties of *W. homomorpha* on types of processes, since different types are often found on the same individual. The tabulation agrees with that for the genus, some of the processes closely following the plate boundary and almost being on it, others being well in from the margins. The number of processes per plate is variable. The lateral, apical and antapical areas can be marked by broad multibranched processes.

Included within *W. homomorpha* are some of the forms described by Pastiels (1948) as *Hystrichosphaeridium geometricum*. Fuller discussion of the *W. homomorpha*/*H. geometricum* complex will be found under *W. homomorpha* var. *quinquelata*.

Wetzeliella* (*Wetzeliella*) *homomorpha var. ***quinquelata*** nov.

Pl. 18, fig. 7

1948. *Hystrichosphaeridium geometricum* Pastiels (pars) : 41, pl. 14, figs. 1, 2, 4, 8, 11.
1961. *Wetzeliella* cf. *ovalis* Eisenack ; Alberti : pl. 1, fig. 13.

DERIVATION OF NAME. Latin, *quinque*, five ; *latus*, side—hence, five-sided.

HOLOTYPE. B.M.(N.H.) slide V.51963(1). London Clay ; Whitecliff, sample WC4.

DIMENSIONS. Holotype : periphragm, length 94μ ; breadth 105μ. Capsule, length 69μ ; breadth 69μ. Observed range : outer shell, length (including horns and processes) 73–94μ, length (excluding horns and processes) 50–72μ, breadth (including horns and processes) 77–105μ, breadth (excluding horns and processes) 53–70μ. Capsule, length 47–69μ ; breadth 50–69μ. Length of processes 7. Number of specimens measured, 7.

DESCRIPTION. This is a variety of *W. homomorpha* having a thin periphragm with a distinctly pentagonal outline. Each angle of the periphragm may be marked by a branched process, larger than the rest, or by a horn not exceeding 20μ in length. When two antapical horns are present, the right is invariably the longer. The enclosed capsule has a pentagonal outline and is closely pressed against the periphragm save at the angles. The capsule wall is usually thin and smooth.

The tabulation is often well shown from the orientation of the processes, which in some specimens are almost restricted to the plate boundary zone in simulate complexes, whilst in others they are more numerous and irregularly arranged. The hollow, simple or branched processes tend to be concentrated on the ambitus of the periphragm. As in the typical *W. Homomorpha*, the processes show considerable variation distally. They are nearly always closed with acuminate, blunt or bifid tips, but several specimens with processes that open distally with aculeate or entire

margins are included since they are identical to *W. homomorpha* var. *quinquelata* in outline, wall thickness and tendency for processes to be concentrated on the ambitus. As is to be expected, intermediate forms exist between *W. homomorpha* and *W. homomorpha* var. *quinquelata*.

OCCURRENCE. Eocene, London Clay ; Whitecliff and Enborne.

STRATIGRAPHIC RANGE. *W. homomorpha* var. *quinquelata* has previously been recorded from the Ypresian of Belgium (Pastiels 1948) and the Upper Eocene of Germany (Alberti 1961).

REMARKS. Pastiels (1948) stated that *H. geometricum* is represented by flattened capsules, roughly pentagonal, of which one of the sides, sometimes concave, is smaller. Unfortunately the name created by Pastiels was pre-occupied by *Hystrichosphaeridium geometricum* Deflandre 1942, for forms with a polygonal test from the Palaeozoic (since transferred to *Veryhacium*). This was pointed out by Deflandre & Cookson (1955), who in erecting *W. homomorpha* compared it to *H. geometricum* (Pastiels) and concluded that the two were probably synonymous. However, in the diagnosis of *W. homomorpha*, Deflandre & Cookson stated that the theca is polygonal, more or less rounded. A detailed study of London Clay forms attributable to the *W. homomorpha–H. geometricum* (Pastiels) complex has shown that there are two extreme forms of common occurrence, firstly pentagonal forms, often with well developed horns, and secondly ovoidal, sub-spherical or rhomboidal forms lacking horns. The two forms can be readily separated, although intermediate types do occur.

Pastiels figured, as within his species, types identical to the two extreme London Clay forms, as well as intermediate specimens, although the holotype of *H. geometricum* (Pastiels) is almost pentagonal and the accompanying description suggests that specimens with a pentagonal outline were the more frequent in the Ypresian. It therefore seems advisable to restrict *W. homomorpha* to the forms having sub-spherical, ovoidal or rhomboidal outline, whilst defining a variety, *W. homomorpha* var. *quinquelata*, to include forms having a pericoel with pentagonal outline with or without horns. This is a workable system in the London Clay and avoids too much infraspecific variation going unheeded.

Wetzeliella* (*Wetzeliella*) *ovalis Eisenack

Pl. 18, fig. 10

1954. *Wetzeliella ovalis* Eisenack : 59, pl. 8, figs. 1–7.

DISCUSSION. The outline of the periphragm of London Clay specimens of *W. ovalis* is variable ; usually it is oval to rhomboidal, but it can be sub-pentagonal, with a fifth side tending to develop when there are two antapical horns. The angle of the sides are developed into small horns, one apical, two lateral and one or two antapical ; when there are two, the right antapical horn is always the longer. The simple or branched processes are intratabular and are uniformly present over all the surface of the pericoel, not as the type material where they are sparse on the dorsal and ventral surfaces. The tabulation of *W. ovalis* is the same as that of *W. articulata*.

The processes vary in width from 1·5–3μ ; they are in contact with the pericoel and are distally open, their margins being aculeate, with up to six aculei arising from a single process. The length of the aculei can be as great as 7μ ; in some specimens they are granular. The nature of the processes distally is one of the diagnostic features of specimens of *W. ovalis* from the London Clay.

The capsule almost completely fills the pericoel, sometimes even exhibiting a protuberance when opposite a horn. Its wall can be smooth or granular. An archaeopyle is commonly present.

DIMENSIONS. Range observed in London Clay : outer shell—length 94–120μ, breadth 77–115μ. Capsule—length 68–79μ, breadth 67–78μ. Number of specimens measured, 7.

OCCURRENCE. Eocene, London Clay ; Whitecliff and Enborne.

STRATIGRAPHIC RANGE. Present in the Oligocene of Germany (Eisenack 1954*b*) and in the London Clay.

Wetzeliella (*Wetzeliella*) *condylos* sp. nov.

Pl. 20, figs. 1, 2

DERIVATION OF NAME. Greek, *kondylos*, knuckle, knob, enlarged end of a bone : referring to the form of the processes.

DIAGNOSIS. Flattened outer shell with well formed lateral horns, low or absent apical horns and two antapical horns, the right one always longer. Apical area tending to be curved. Periphragm ornamented with a number of extremely short, blunt intratabular processes some arranged in simulate complexes reflecting a tabulation of 4′, 3a, 7″, xc, 5‴, 2⁗, 3s, others occurring within complexes. Hypotract of periphagm of greater length than epitract. Capsule ovoidal to sub-circular in outline ellipsoidal in cross section. Endophragm up to 3·5μ thick, surface smooth or undulating.

HOLOTYPE. B.M.(N.H.) slide V.51967. London Clay ; Sheppey, Kent, sample Sh.2.

DIMENSIONS. Holotype : Periphragm, length 122μ, breadth 112·5μ. Observed range : outer shell, length 76–122μ, breadth 86–115μ. Capsule, length 56–85μ ; breadth 62–85μ. Number of specimens measured, 6.

DESCRIPTION. The periphragm of *W. condylos* is up to 3μ thick and forms the extremely small processes. These open to the pericoel and are cylindrical in cross section and distally closed with a blunt ending. The height of the processes is of the order of 1–3μ. The characteristic generic tabulation can be determined from the regular disposition of the processes in simulate complexes on the pericoel. Auxiliary irregularly arranged processes are also common. The lateral horns of the periphragm are always prominently developed ; the apical horn, if present, is at the most a small protuberance. The capsule occasionally abutts on to the inner surface of the periphragm.

OCCURRENCE. Eocene, London Clay ; Sheppey.

REMARKS. Only two described species of *Wetzeliella*, *W. lineidentata* Deflandre & Cookson, 1955 (Lower Tertiary, Australia) and *W. irtyschensis* Alberti, 1961 (Oligocene, U.S.S.R.) have processes of a similar nature to those of *W. condylos*. *W. lineidentata* was originally based on a single damaged specimen, the apical region of which was absent. Cookson & Eisenack (1961) however, discovered beautifully preserved complete specimens of this species from the Lower Tertiary of Western Australia. *W. lineidentata* differs from *W. condylos* in having lateral horns which arise in a medial position, a hypotract and epitract of similar size, the epitract of the outer shell having a triangular outline ; the capsule outline. The two species appear to be closely related however. *W. irtyschensis* differs from *W. condylos* in having poorly developed lateral horns and two antapical horns of equal length.

Wetzeliella* (*Wetzeliella*) *similis Eisenack

Pl. 20, fig. 5

1954. *Wetzeliella similis* Eisenack : 58, pl. 8, figs. 8–10.
1961. *Wetzeliella* cf. *similis* Eisenack ; Gerlach : 154, pl. 25, fig. 5.

DISCUSSION. *W. similis* is interpreted from Eisenack's diagnosis, as a species of *Wetzeliella* having a broad low apical horn ; long, drawn out lateral horns ; and one antapical horn, which lies to the right of the midventral line, whilst to the left the other antapical horn is represented only by a low protuberance. The figures accompanying *W. similis* in Eisenack (1954) are unfortunately too poor to give any further help in recognition of the species, although one specimen he figured (pl. 8, fig. 9) has an apical opening and must be considered to belong to a genus other than *Wetzeliella*.

W. similis is a species intermediate between *W. articulata* and *W. solida* (Gocht) (pars) Eisenack 1961, the former having a well developed apical and two antapical horns, the latter possessing only one well developed antapical horn, whilst an apical horn is absent. Attempts to set up a varietal name of *W. similis* for forms with very reduced apical horns have proved fruitless in the London Clay, intergradation being so gradual that it is impossible to distinguish any dividing line. It is therefore considered more advisable to extend the limits of *W. similis* to include forms with apical horns less than 7μ long. Forms with apical horns below 6μ would be placed in *Wetzeliella solida*. The apical horn of *W. similis* usually merges imperceptibly into the outline of the epitract ; it can occasionally be more sharply delimited. The single specimen described and figured by Gerlach (1961) is here included in *Wetzeliella* (*W.*) *similis*.

Examples of *Wetzeliella* (*W.*) *similis* from the London Clay have an apical horn which is considerably broader and lower than that of *W. articulata*, whilst the indented lateral horns are long and drawn out. The right antapical horn is always longer than the apical horn. The left antapical horn is represented by a slight bulging of the pericoel. The breadth/length ratio of the outer shell generally

exceeds 1 to 1. The slender, simple or branched processes are hollow, open distally with an aculeate margin, the aculei being patulate, orthogonal or even recurved. The processes reflect a tabulation agreeing with that of the type species *W. articulata*. The processes become shorter towards the horns. The periphragm can be up to 1/2μ thick, and it is always smooth.

The capsule is ovoidal or subcircular in outline, ellipsoidal in cross section. It lies at a variable distance from the inner surface of the periphragm, and has a wall up to 2μ thick, which may be smooth or granular. Commonly observed in specimens of *Wetzeliella* (*W.*) *similis* is a local thickening of the endophragm directly opposite the point of origin of the horns. The significance of this may be that the horns are points of weakness within the cyst.

DIMENSIONS. Outer Shell, length 100–158μ, breadth 117–166μ. Capsule, length 65–97·5μ, breadth 66–92μ. Length of processes 8–18μ. Number of specimens measured, 15.

OCCURRENCE. Whitecliff and Enborne.

STRATIGRAPHIC RANGE. Oligocene of Germany (Eisenack 1954) and the London Clay.

Wetzeliella (Wetzeliella) solida (Gocht) comb. nov.

1955 *Dracodinium solidum* Gocht (pars) : 88–91, text-figs. 3*a*, *b*, 4*a*, *b*, 5*a*.
1961 *Wetzeliella* (*Dracodinium*) *Solida* (Gocht) Eisenack : 306.

DISCUSSION. Only a few specimens of *W. Solida* have been recorded from the London Clay. They are characterised by the absence of an apical horn. The surface of the periphragm bear slender, simple or branched processes that distally have an aculeate margin. The processes on the ambitus of the periphragm are often the shortest. The archeopyle is intercalary, the tabulation is the same as in other species of *Wetzeliella* with the apicals being reduced in size.

Gocht (1955) erected the genus *Dracodinium* on the single species *D. solidum* and distinguished it from *Wetzeliella* on the absence of an apical horn. Within the species *D. solidum* he unfortunately included two distinct forms, those with intercalary archeopyles and others with an apical archeopyle. Since the emended diagnosis of *Wetzeliella* excludes forms with an apical archeopyle, Gocht's latter type needs transferring to a new genus, whilst the forms with the intercalary archeopyle are included within the genus *Wetzeliella* as *W. solida*.

DIMENSIONS. Periphragm, length 105–117μ, breadth 117·5–137μ. Capsule, length 68–76μ, breadth 69–82μ. Number of specimens measured, 5.

OCCURRENCE. Whitecliff and Enborne.

STRATIGRAPHIC RANGE. *W. solida* has previously been recorded from the Eocene or Oligocene? of Germany (Gocht 1955). The forms classed as *Dracodinium Solidum* by Alberti (1961, pl. 1, fig. 9) appear to be another as yet unnamed species.

Wetzeliella* (*Wetzeliella*) *symmetrica Weiler

Pl. 20, fig. 6

1956. *Wetzeliella symmetrica* Weiler : 132, pl. 11, figs. 1–3 ; text-figs. 2–5.
1963. *Wetzeliella symmetrica* Weiler ; Brosius, pl. 2, fig. 7.

DISCUSSION. This species is characterized by a periphragm with rhomboidal outline, the angles of which are prolonged into more or less equally long horns. The single antapical horn sits astride the mid-ventral line. The processes commonly have aculeate distal margins or can be bifurcate.

DIMENSIONS. Range observed in London Clay : outer shell, length 125–167μ, breadth 115–148μ. Capsule, length 70–97μ, breadth 66–88μ. Number of specimens measured, 7.

OCCURRENCE. Eocene, London Clay ; Whitecliff, Enborne, Studland and Sheppey. *Wetzeliella* (*W.*) *symmetrica* has also been recorded from the Oligocene of Germany (Weiler 1956, Alberti 1961, Gerlach 1961 and Brosius 1963).

Wetzeliella* (*Wetzeliella*) *symmetrica var. ***lobisca*** nov.

Pl. 20, fig. 3

1948. *Hystrichosphaeridium articulatum* Pastiels : 43, pl. 4, figs. 13, 17.
1961. *Wetzeliella symmetrica symmetrica* Gerlach : 185, pl. 25, figs. 7, 8.

DERIVATION OF NAME. Latin ; *lobisca*, a small protuberance.

HOLOTYPE. B.M.(N.H.) slide V.51970. London Clay ; Sheppey, Kent, sample 1.

DIMENSIONS. Holotype : outer shell, length 137μ, breadth 123μ. Capsule, length 78μ, breadth 70μ. Observed range : outer shell, length 125–137μ, breadth, 118–150μ. Capsule, length 72–80μ, breadth 70–79μ. Number of specimen, measured, 4.

DESCRIPTION. This is a variety of *W.* (*W.*) *symmetrica* which has a slightly reduced apical horn and the single antapical horn is offset to the right of the mid-ventral line. It is identical with the two figured specimens of *W. symmetrica symmetrica* Gerlach (1961) and *Hystrichosphaeridium articulatum* Pastiels (1948).

OCCURRENCE. Eocene, London Clay ; Whitecliff, Enborne and Sheppey. It has also been recorded from the Ypresian of Belgium (Pastiels 1948 as *H. articulatum*) and the Oligocene–Miocene of Germany (Gerlach 1961).

Wetzeliella* (*Wetzeliella*) *varielongituda sp. nov.

Pl. 20, figs. 4, 8

DERIVATION OF NAME. Latin ; *varius*, varied, *longituda*, length.

DIAGNOSIS. Periphragm outline sub-rhomboidal, with short broad lateral horns, a short wide apical horn and one well developed (right) antapical horn. Left

antapical horn represented by slight protuberance on left antapical margin. Capsule thick walled, often coarsely granular. Processes extremely short on ambitus of periphragm and increasing in length further away from ambitus. Distally processes bifid, aculeate, acuminate or evexate.

HOLOTYPE. B.M.(N.H.) slide V.51973. London Clay ; Sheppey, Kent, sample 2.

DIMENSIONS. Holotype : outer shell, length 103μ, breadth 100μ. Capsule, length 73μ, breadth 71μ. Observed range : outer shell, length 96–126μ, breadth 90–125μ. Capsule, length 64–79μ, breadth 63–84μ. Length/breadth ratio of pericoel 1–1 to 1·1–1. Number of specimens measured, 7.

DESCRIPTION. One of the diagnostic features of *W. varielongituda* are the processes. The wall of the periphragm is up to 1/2μ in thickness, so that the slender processes have only a minute central tubule, along their length. They are distally closed, proximally open to the pericoel. The processes can be granular and are always simple. The shortest processes occur on the ambitus of the pericoel and particularly is this so on the lateral horns and epitract. It is these processes that can be acuminate or evexate distally. The processes are regularly orientated in simulate complexes or are irregular occurring within the complexes. Typical *Wetzeliella* tabulation is decipherable, with the archeopyle intercalary.

The horns of *W. varielongituda* tend to be broad and low, merging imperceptibly with the lateral margins of the periphragm. This is especially so with the apical horn.

The capsule is sub-circular in outline, ellipsoidal in cross section and has a wall up to 3·5μ thick. The wall often shows local thickening directly opposite the horns. Distance of the capsule from the inner surface of the periphragm is variable.

OCCURRENCE. Eocene, London Clay ; Sheppey, Kent.

REMARKS. The nature of the processes, outline of the pericoel and structure of the capsule readily distinguish *Wetzeliella* (*W.*) *varielongituda* from other species of *Wetzeliella*.

Sub-Genus ***WETZELIELLA (RHOMBODINIUM)*** Gocht 1955

DIAGNOSIS. A sub-genus of the genus *Wetzeliella* that does not possess processes on the periphragm. Tabulation indistinctly shown apart from a transverse cingulum.

TYPE SPECIES. *Wetzeliella* (*Rhombodinium*) *draco* (Gocht 1955). Oligocene ; Germany.

Wetzeliella (Rhombodinium) glabra Cookson

Pl. 20, figs. 9, 10

1956. *Wetzeliella glabra* Cookson : 186, pl. 2, figs. 1–5.

DISCUSSION. Specimens of *W. glabra* from the London Clay differ from the type material in having only one well developed antapical horn, the right. The left antapical horn is, at the most, represented by a slight protuberance. The transverse

girdle is also less well marked whilst the capsule archaeopyle gives the impression of being apical in some specimens. This may be due to secondary movement of the capsule within the pericoel. The capsule is occasionally found free.

On the outer surface of the periphragm of some individuals are present dendritic ridges, radiating out from central points and being up to 10 or 15μ across. They are not caused by local thickenings of the wall but by undulations. On an individual there can be a large number of these dendritic radiating structures. They are possibly a result of fungal attack. *W. glabra* is included in the sub-genus *Rhombodinium* on account of the absence of processes.

DIMENSIONS. Range observed in London Clay : outer shell, length 140–151μ, breadth 147–168μ. Capsule, length 66–80μ, breadth 69–76μ. Number of specimens measured, 6.

OCCURRENCE. Eocene, London Clay ; Sheppey, Kent. Eocene ; Australia (Cookson 1956).

X. FURTHER DINOFLAGELLATE CYSTS FROM THE SPEETON CLAY

By W. A. S. SARJEANT

INTRODUCTION

The assemblages of dinoflagellate cysts from the Speeton Clay are both extremely rich and extremely varied. Their description was begun in a previously published paper (Neale & Sarjeant 1962) and a number of species are here dealt with, wherever appropriate, in earlier chapters. All remaining species represented that have been studied to date are described in this chapter, and the stratigraphical distribution of all the constituent species of the assemblages is summarized in tabular form and discussed.

Genus ***NETRELYTRON*** Sarjeant 1961*a* : 113

EMENDED DIAGNOSIS. Cavate dinoflagellate cysts, enclosing body spindle-shaped, inner body ovoidal to spindle-shaped. Shell showing no trace of tabulation or of cingulum or sulcus. Shell enclosed in cloak of adherent organic matter, formless or oval to spindle-shaped in outline : fragments of mineral matter and other sedimentary debris sometimes embedded in cloak. Archaeopyle frequently developed : precingular in position.

TYPE SPECIES. *Netrelytron stegastum* Sarjeant 1961*a*. Upper Jurassic (Oxfordian) ; England.

REMARKS. This genus is characterized by its shape, cavate character and investing mass of organic matter ; formation of a similar debris cloak during encystment is known to occur in some modern dinoflagellates.

The genus *Kalyptea* Cookson & Eisenack 1960*b* from the Upper Jurassic of Australia, is described as having a " diaphanous veil-like external membrane ", which may correspond to the organic cloak of *Netrelytron* ; the cysts are oval, with one to two horns, but lack an inner body. The somewhat similar genus *Komewuia* Cookson & Eisenack 1960*b*, also from the Upper Jurassic of Australia, lacks either outer cloak or inner body.

Netrelytron trinetron sp. nov.

Pl. 22, fig. 3 ; Text-fig. 51

DERIVATION OF NAME. Greek, *tri-*, three ; *netron*, spindle : referring to the similar shapes of the debris cloak and the enclosing and inner bodies.

DIAGNOSIS. A *Netrelytron* with outer body of basically ovoidal shape, giving rise to strongly tapering, conical apical horn and somewhat shorter, conical antapical horn. Shape of inner body exactly similar. Horns polar and axial in position and direction. Endophragm and periphragm minutely, but densely, granular.

HOLOTYPE. B.M.(N.H.) slide V.51729(1). Speeton Clay, Shell West Heslerton Borehole at 39 metres depth, West Heslerton, Yorks. Lower Cretaceous (Middle Barremian).

DIMENSIONS. Holotype—overall length of enclosing body 90μ, breadth 53–5μ, length of apical horn 18μ, of antapical horn 5μ ; overall length of inner body 67·5μ, breadth 38·5μ. Range of dimensions ; overall length of enclosing body c.70–95μ.

DESCRIPTION. The holotype is enclosed in a spindle-shaped cloak of debris : in other specimens, the debris cloak appears less well formed.

The outer membrane is spindle-shaped, with unequally developed horns. In the holotype, the apical horn tapers sharply to an acute point from about mid-length : this was not the case in other specimens, where the apical horn tapered more smoothly from base to tip. The inner body is of comparable shape, its apical horn always tapering smoothly from base to tip.

No specimen seen shows a well-developed archaeopyle ; however, the holotype shows a slit, corresponding in position to a precingular opening, which may be an archaeopyle that has either incompletely opened or subsequently closed up.

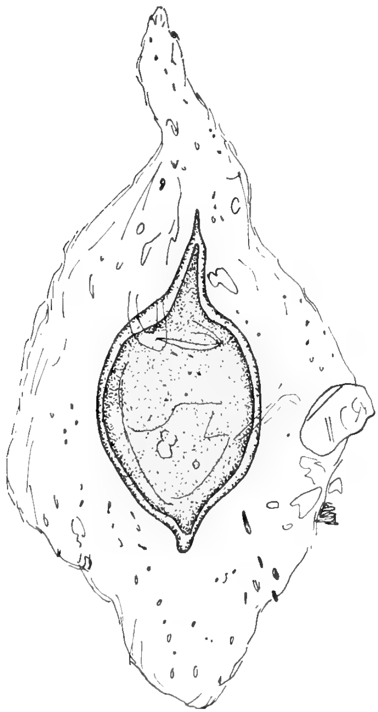


Fig. 51. *Netrelytron trinetron* sp. nov., showing the shell surrounded by the enclosing cloak of organic matter. × c. 500.

REMARKS. In the form of the inner body, *Netrelytron trinetron* sp. nov. differs from both other described species of the genus. It has only been recorded to date from one horizon in the West Heslerton Bore, from which some six specimens have been recorded.

OTHER SPECIES

Netrelytron jurassicum (Alberti 1961) from the Middle Jurassic (Bathonian–Callovian) of Germany, is here transferred to this genus from *Kalyptea* on the basis of its possession of an inner body within the spindle-shaped shell.

Brosius (1963 : 38, pl. 3, fig. 2, pl. 4, fig. 2, pl. 5, fig. 4) has described a species from the German Oligocene, as *Netrelytron* sp. nov. This corresponds in most particulars to the emended diagnosis of *Netrelytron*, but lacks a cloak of debris. Erection to separate generic status may prove appropriate.

Genus ***PARANETRELYTRON*** nov.

DERIVATION OF NAME. Greek, *para*, near ; *netron*, spindle ; *elytron*, sheath, husk—refers to the similarity of this genus to *Netrelytron*.

DIAGNOSIS. Cavate dinoflagellate cysts, enclosing body spheroidal to ovoidal with apical horn ; inner body spheroidal. Shell lacking tabulation, with or without traces of cingulum. Shell enclosed in cloak of adherent matter, formless to oval in outline ; fragments of mineral matter and other sedimentary debris sometimes embedded in cloak. Archaeopyle formation not known.

TYPE SPECIES. *Paranetrelytron strongylum* sp. nov. Lower Cretaceous (Lower Barremian) ; England.

REMARKS. This genus differs from *Netrelytron* in lack of an antapical horn and in presence of indications of a cingulum ; and from all other described genera in the possession of an outer cloak of organic debris.

Paranetrelytron strongylum sp. nov.

Pl. 21, fig. 5 ; Pl. 23, fig. 5 ; Text-fig. 52

DERIVATION OF NAME. Greek, *strongylos*, round, rounded.

DIAGNOSIS. A *Paranetrelyton* having a spheroidal outer body tapering smoothly to form short, blunt apical horn. Inner body spheroidal and relatively large, thin-walled and often hard to distinguish. A poorly-marked cingulum sometimes present. Endophragm and periphragm smooth or only very minutely granular.

HOLOTYPE. B.M.(N.H.) slide 51722(1). Speeton Clay, Shell West Heslerton Borehole at 42·5 metres depth, West Heslerton, Yorks. Lower Cretaceous (Lower Barremian).

DIMENSIONS. Holotype : overall length 56μ, breadth 45μ, length of apical horn 10μ ; length of inner body c.40μ, breadth c.40μ. Range of dimensions : overall lengths 51–58μ.

DESCRIPTION. The holotype is enclosed in a roughly oval cloak of debris ; in the three other specimens observed to date, the debris cloak was comparable. The enclosing body is roughly lemon-shaped. The inner body fits quite closely, except at the apical end where there is a quite large expansion of the pericoel. It is thin and transparent and, as a result, very hard to distinguish ; its presence was confirmed only under phase contrast.

The debris cloak of the holotype contains a ball-like mass of debris immediately posterior to the antapex. This structure is of doubtful significance and may simply represent fortuitous adherence of organic debris from a quite unrelated source. An archaeopyle has not been observed to date.

REMARKS. *Paranetrelytron strongylum* sp. nov. occurs in the 39 and 42·5 metres horizons in the West Heslerton Borehole (Lower to Middle Barremian). Its small size and debris cloak render it especially inconspicuous ; further studies may well indicate a much wider distribution.

Genus ***MUDERONGIA*** Cookson & Eisenack 1958 : 40

TYPE SPECIES. *M. mcwhaei* Cookson & Eisenack 1958. Lower Cretaceous (Aptian) ; Australia.

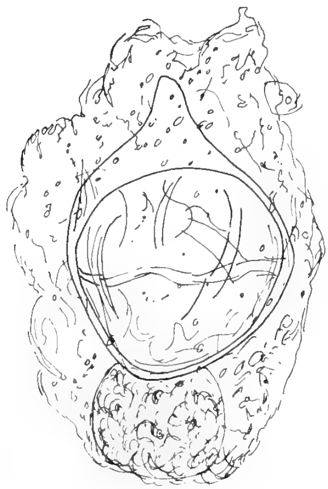


FIG. 52. *Paranetrelytron strongylum* sp. nov., showing the shell surrounded by the enclosing cloak of organic matter. × c. 750.

Muderongia staurota sp. nov.

Pl. 21, figs. 6, 7 ; Pl. 23, fig. 4 ; Text-fig. 53

DERIVATION OF NAME. Greek, *staurotos*, cruciform.

DIAGNOSIS. A *Muderongia* having an ovoidal to ellipsoidal enclosing body, prolonged into four strong horns. Apical horn strong and tapering, length slightly less than length of shell alone. Lateral horns quite short, less than shell breadth, at first almost parallel sided, but at about one-third length, anterior margin tapering backward to form an angle with posterior margin. Antapical horn basically conical, with slight out-bulge at one side ; length also less than length of shell alone. Inner body ovoidal to ellipsoidal. Periphragm smooth or finely pitted ; endophragm varying from smooth to densely granular. Shell showing neither trace of tabulation nor of cingulum or sulcus. An apical archaeopyle is formed.

HOLOTYPE. B.M.(N.H.) slide V.51724(3). Speeton Clay, Shell West Heslerton Borehole at 42·50 metres depth, West Heslerton, Yorkshire. Lower Cretaceous (Lower Barremian).

PARATYPE. B.M.(N.H.) slide V.51718(3). Same locality and horizon.

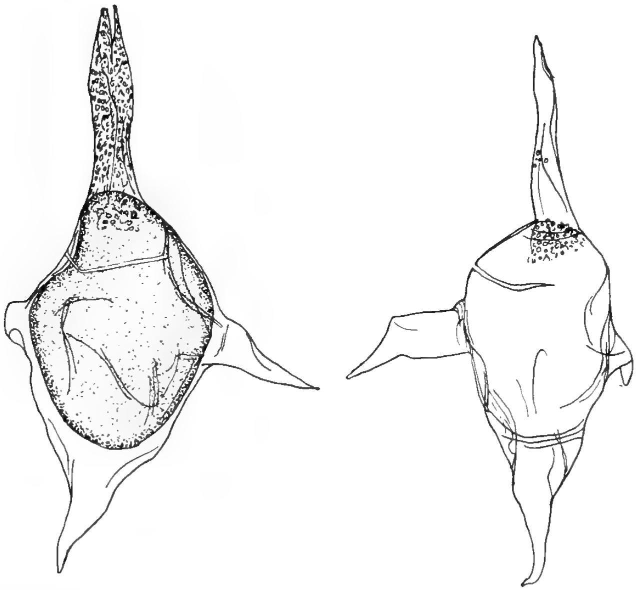


FIG. 53. *Muderongia staurota* sp. nov. Left, holotype. Right, paratype. The variation in proportions and in degree of granularity of the inner body is shown : the holotype shows incipient formation of an archaeopyle. × c. 500.

DIMENSIONS. Holotype—overall length 170μ, breadth 93μ; length of apical horn (tip missing) 55μ, of antapical horn 34·5μ, of longer lateral horns 26μ, length of inner body, 70μ, breadth 55μ. Paratype—overall length 145μ, breadth 80μ; length of apical horn, 47μ, of antapical horn, c.44μ, of longer lateral horns c.31μ; length of inner body c.56μ, breadth c.51μ. These two specimens represent opposite extremes of the observed range of variation.

DESCRIPTION. The enclosing body has a basically cruciform outline, with a distinctly oval shell enclosing, more or less tightly, an inner body of similar shape. The lateral horns show no distinct notch, nor is a second, shorter antapical horn developed; however, the backward curve of the lateral horns and the lateral bump on the antapical horn suggest affinity to species showing these features.

The periphragm shows some degree of pitting, variable in degree and location but usually especially dense on the apical horn. The inner body varies from smooth to granular; where it is smooth, the inner body becomes hard to distinguish and may only be confirmed under phase contrast. (The holotype and paratype illustrate this variation.)

This species is relatively common in the Lower Barremian of the West Heslerton Borehole : over 20 specimens were noted, of which the majority comprised either detached apices or shells lacking an apex, complete shells being relatively infrequent. Both holotype and paratype show incipient development of an archaeopyle.

REMARKS. *Muderongia staurota* sp. nov. is characterized by the morphology of its shell processes. In contrast *M. mcwhaei* has a pronouncedly rhombic shell outline; proportionately longer and slimmer horns; notched lateral horns and a second, short antapical horn. *M. simplex* Alberti 1961, from the Lower Cretaceous (Hauterivian to Valanginian) of Germany and Bulgaria, has short horns of almost equivalent relative length, the lateral horns being blunt and notched, and a second antapical horn being again developed. *M. perforata* Alberti 1961, from the Upper Cretaceous (Turonian) of Germany, has very strong, thick horns, the second antapical horn being especially pronounced. *M. tetracantha* (Gocht 1957), from the Lower Cretaceous (Hauterivian) of Germany, has in contrast extremely long and delicate horns; a second antapical horn is lacking, but the notching of the lateral horns is so deep as to approach bifurcation into unequal branches. *M. tomaszowensis* Alberti 1961, from the Lower Cretaceous (Valanginian) of Germany and Poland, has stubby apical and antapical horns and blunt notched lateral horns. *M. crucis* Neale & Sarjeant 1962, from the Lower Cretaceous (Hauterivian) of England, is extremely large (overall length 250–325μ), with long axial horns and long lateral horns, the latter backswept and not notched.

Genus *APTEODINIUM* Eisenack 1958*c*

TYPE SPECIES. *A. granulatum* Eisenack 1958*c*. Lower Cretaceous (Aptian); Germany.

Apteodinium maculatum Eisenack & Cookson

Pl. 22, fig. 1 ; Text-fig. 54

1960. *Apteodinium maculatum* Cookson & Eisenack : 4, pl. 2, figs. 1–3.

REMARKS. This species, hitherto recorded only from the Lower Cretaceous (Aptian to Albian) of Australia, occurs in low numbers in the assemblages from the Shell West Heslerton Borehole, West Heslerton, Yorkshire, at 42·50 metres depth. (Lower Barremian).

The English specimens are somewhat smaller than the Australian type material : the figured specimen (B.M.(N.H.) slide V.51718(4)), with overall length 75μ, breadth 64μ, falls a little below the quoted Australian range of length 74–105μ, breadth 70–105μ. There are faint indications of a sulcus and the " small thickened areas with circular outlines " noted by Eisenack and Cookson are totally lacking. Nor has an archaeopyle been observed to date. (The " hoof-shaped pylome " mentioned by those authors must be interpreted as a precingular archaeopyle.) However, the triviality of these differences and the complete correspondence in other characters does not justify any nomenclatural distinction of the English specimens, which accordingly represent a considerable extension in the geographic and stratigraphic range of this species.

Genus ***DOIDYX*** nov.

DERIVATION OF NAME. Greek, *doidyx*, pestle, in reference to the shell shape.

DIAGNOSIS. Proximate dinoflagellate cysts with flattened biconical shell, pronouncedly asymmetical. Epitract in form of high cone which may be drawn out into an apical horn, giving a mammillate appearance : hypotract in form of flattened cone, with or without antapical prominence. Shell bulging out laterally to one side more than to the other ; lateral horns lacking. Greater part of shell surface covered

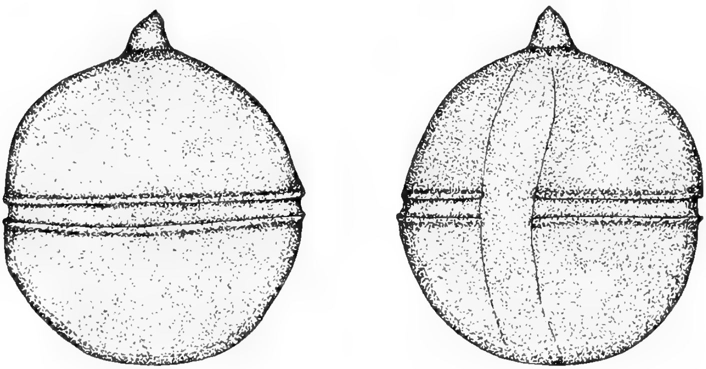


FIG. 54. *Apteodinium maculatum* Eisenack & Cookson, showing the dense granulosity and the positions of cingulum and sulcus. × c. 800.

with short spines, simple or bifurcate : arrangement is in general random, but sometimes in rows, suggesting traces of tabulation. Equatorial zone, corresponding to cingulum, lacking spines : not hollowed. No pattern of sutures visible, no clear indication of sulcus. Apical archaeopyle formed by schism of shell on angular line of breakage.

TYPE SPECIES. *Doidyx anaphrissa* sp. nov. Lower Cretaceous (Lower Barremian) ; England.

REMARKS. In its asymmetrically biconical shell, spine cover and absence of tabulation, this new genus differs from all described fossil genera. The asymmetry and mode of archaeopyle formation suggests a probable derivation from the genus *Pseudoceratium* by reduction of polar horns and loss of the lateral horn.

Doidyx differs from *Diconodinium*, *Palaeohystrichophora* and *Dioxya* in its asymmetrical shape : from *Diconodinium* also in the absence of a sulcus : from *Palaeohystrichophora* also in the lack of an inner body ; and from *Dioxya* in the clear indication of a cingulum. It differs from the superficially similar genus *Aptea* in the lack of an enclosing membrane.

Doidyx anaphrissa sp. nov.

Pl. 22, fig. 8 ; Pl. 23, fig. 6 ; Text-fig. 55

DERIVATION OF NAME. Greek, *anaphrisso*, to bristle.

DIAGNOSIS. A *Doidyx* having an asymmetrically biconical shell with short, blunt apical horn and with low bump on antapex. Spines simple, capitate or briefly bifurcate. Portion thrown off in archaeopyle formation exceeding one-third of shell length.

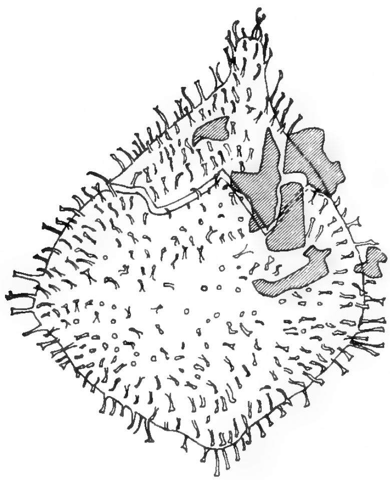


FIG. 55. *Doidyx anaphrissa* sp. nov. Holotype, showing archaeopyle formation. × c. 750.

HOLOTYPE. B.M.(N.H.) slide V.51723(3). Speeton Clay, Shell West Heslerton Borehole, West Heslerton, Yorks., at 42·5 metres depth. Lower Cretaceous (Lower Barremian).

DIMENSIONS. Holotype—overall length 105μ, breadth 118μ ; shell length 11μ, breadth 102μ ; spines c.7μ long. Range of dimensions : overall lengths c.120–145μ, breadths c.105–130μ.

DESCRIPTION. This species is moderately abundant, some 25 specimens having been encountered ; complete shells were infrequent, detached apices and shells lacking an apex being commoner.

The shell is approximately club-shaped : its asymmetry is so pronounced that a longitudinal division would leave some 60% on one side, some 40% on the other. The epitract slopes smoothly into the apical horn; the hypotract is surmounted by an antapical bulge of small height and larger amplitude. The surface is very minutely granular.

There is a dense cover of short spines, most often capitate, less frequently evexate, oblate, bifid or bifurcate : these sometimes suggest arrangement into lines, but no coherent pattern was determined. An equatorial belt of moderate breadth, corresponding to the cingulum, lacks spines : a sulcus is not distinguishable.

The holotype shows fission to form an archaeopyle, which has however, not become detached. Its margin is distinctly angular, suggesting a tabulation pattern not otherwise indicated.

REMARKS. In its combination of shape, process cover and mode of archaeopyle formation, *Doidyx anaphrissa* sp. nov. differs from all other described species.

Genus ***BROOMEA*** Cookson & Eisenack 1958 : 41

TYPE SPECIES. *B. ramosa* Cookson & Eisenack 1958. Middle–Upper Jurassic ; Australia.

?***Broomea longicornuta*** Alberti

Pl. 21, fig. 1

1961. ?*Broomea longicornuta* Alberti : 27, pl. 5, figs. 18–21, pl. 6, figs. 1, 2.

REMARKS. This species, originally described from the Lower Cretaceous (Hauterivian–Upper Barremian) of Germany, is represented by a single specimen in the assemblage from the Speeton Clay of the West Heslerton Borehole at 19·25 metres depth (Upper Barremian). The dimensions of this specimen, B.M.(N.H.) slide V.51733(1), are overall length c.285μ ; shell length 100μ, breadth 48μ ; length of apical horn c.130μ ; length of unbent antapical horn 55μ. This falls within the range of overall lengths quoted by Alberti (248–298μ).

Genus *ODONTOCHITINA* Deflandre 1935*a* : 234

TYPE SPECIES. *Ceratium* (*Euceratium*) *operculatum* O. Wetzel 1933. Upper Cretaceous ; Germany.

Odontochitina operculata (O. Wetzel)

Pl. 21, fig. 2

1933. *Ceratium* (*Euceratium*) *operculatum* O. Wetzel : 170, pl. 11, figs. 21–22.
1935. *Odontochitina silicorum* Deflandre : 234, pl. 10, figs. 8–10.
1937. *Odontochitina silicorum* Deflandre ; Deflandre : 47, pl. 18, figs. 8–10.
1946. *Odontochitina operculata* (O. Wetzel) Deflandre, cards 1016-19.
1948. *Palaeoceratium operculatum* (O. Wetzel) O. Wetzel : ?342.
1950. Dreihörnige Hüllen mit Stachelkleid, O. Wetzel : 170, pl. 13, fig. 6.
1952. *Odontochitina operculatum* (O. Wetzel) ; Firtion : 160, pl. 8, fig. 9.
1955. *Odontochitina operculata* (O. Wetzel) ; Deflandre & Cookson : 291, pl. 3, figs. 5, 6.
1955. *Odontochitina operculata* (O. Wetzel) ; Deflandre-Rigaud : 19.
1955. *Odontochitina operculata* (O. Wetzel) ; Valensi : 594, pl. 4, fig. 7.
1958. *Odontochitina operculata* (O. Wetzel) ; Eisenack : 393, pl. 27, figs. 7, 8.
1959. *Odontochitina operculata* (O. Wetzel) ; Gocht : 64, pl. 6, fig. 12.
1961. *Odontochitina operculata* (O. Wetzel) ; Alberti : 30, pl. 6, figs. 6–9.
1961. *Odontochitina operculata* (O. Wetzel) ; Eisenack : 323, pl. 36, fig. 3.
1962. *Odontochitina silicorum* Deflandre ; Pocock : 78, pl. 14, figs. 211, 212.
1963. *Odontochitina operculata* (O. Wetzel) ; Górka : 35, pl. 4, figs. 1–5.
1963. *Odontochitina operculata* (O. Wetzel) ; Balteș : 584, pl. 5, figs. 1–4.
1964. *Odontochitina operculato* (O. Wetzel) ; Singh : 147, pl. 20, figs. 9, 10.

REMARKS. This species is long-ranging and widespread : it has been recorded from the Upper Jurassic of Canada by Pocock (1962) and has a well-documented range in the Cretaceous, from Upper Hauterivian to Campanian. It is present in low numbers in the assemblages from 19·25 metres depth in the Shell West Heslerton Borehole (Upper Barremian). All specimens seen lacked the apex ; the figured specimen, B.M.(N.H.) slide V.51730(4), is the best-preserved, having an overall length of 133·5μ, breadth 88μ, the central body being 53μ long and 48μ broad, the lateral horn c.55μ long and the antapical horn 83·5μ long. The range in dimensions observed was overall lengths 120–133·5μ, breadths 67–100μ : these fall well within the previously quoted ranges. Detached horns, probably of *O. operculata*, were also observed.

Odontochitina operculata is also present at all levels in the Cenomanian of the H.M. Geological Survey Borehole at Fetcham Mill, Surrey.

Genus *FROMEA* Cookson & Eisenack 1958 : 55

TYPE SPECIES. *Fromea amphora* Cookson & Eisenack 1958. Cretaceous (Aptian to Cenomanian) ; Australia.

Fromea amphora Cookson & Eisenack

Pl. 22, fig. 4 ; Pl. 23, fig. 3

1958. *Fromea amphora* Cookson & Eisenack : 56, pl. 5, figs. 10, 11.
1961. *Fromea amphora* Cookson & Eisenack ; Alberti : 23, pl. 12, fig. 13.
?1961. Chrysomonadiniae? Maliavkina *et al.*, pl. 52, figs. 1–5.

REMARKS. This species, originally described from somewhat higher horizons in Australia, has been recorded by Alberti from the Upper Barremian of Germany and occurs at this level in the Shell West Heslerton Borehole (at 19·25 metres depth). The figured specimens, B.M.(N.H.) slide V.51732(1, 2), are of closely similar size, respectively measuring 84 × 49μ and 84 × 50μ, the apex being lacking ; this is within the range quoted for the Australian specimens (62–95μ × 47–81μ) and larger than that quoted for the German specimens (58–66μ × 49–52μ).

The shell surface is minutely granular in these specimens ; there is little indication of a cingulum.

The specimens figured by Maliavkina et al. (1961, pl. 52, figs. 1–5), from the Maestrichtian of Siberia, may be examples of *Fromea amphora*, but are rather small.

Genus *SYSTEMATOPHORA* Klement 1960 : 61

TYPE SPECIES. *S. areolata* Klement 1960. Upper Jurassic (Kimmeridgian) ; Germany.

Systematophora schindewolfi (Alberti)

Pl. 22, fig. 5

1961. *Hystrichosphaerina schindewolfi* Alberti : 38, pl. 10, figs. 1–3, 6, 7.
1962. *Systematophora schindewolfi* (Alberti) Neale & Sarjeant : 455 (by implication).

REMARKS. This species, originally described from the Cretaceous (Upper Barremian to ?Senonian) of Germany, has been encountered only in the horizon from 42·5 metres depth in the Shell West Heslerton Borehole (Middle Barremian). The majority of examples are too obscured or badly positioned for study, but one specimen, B.M.(N.H.) slide V.517121(1), was excellently preserved and favourably orientated. Its dimensions (overall length 120μ, breadth 112μ ; shell length 65μ, breadth 60μ) accord with those quoted by Alberti (shell length 58–70μ ; length of appendages 22–39μ).

Study showed that the distribution of the annular process complexes on epitract and hypotract, and the linear equatorial complexes, was precisely that specified for the genus by Klement.

Genus *GARDODINIUM* Alberti 1961 : 18

TYPE SPECIES. *Gardodinium eisenacki* Alberti 1961. Lower Cretaceous (L. Hauterivian to Aptian) ; Germany.

Gardodinium eisenacki Alberti

Pl. 21, fig. 4

1961. *Gardodinium eisenacki* Alberti : 18, pl. 3, figs. 8–13.

REMARKS. This species occurs in moderate abundance in the assemblages from 39 metres and 42·5 metres depth. Specimens are frequently distorted. The figured specimen, B.M.(N.H.) slide V.51726(1), is the best preserved ; its dimensions are overall length 76μ, breadth 55μ ; shell length 56μ, breadth 50μ. The range of dimensions exhibited accords closely with that quoted by Alberti (77–85μ × 55–60μ overall).

Genus ***DINGODINIUM*** Cookson & Eisenack 1958 : 39

TYPE SPECIES. *Dingodinium jurassicum* Cookson & Eisenack 1958. Upper Jurassic ; Papua and Australia.

?Dingodinium albertii sp. nov.

Pl. 21, fig. 3, Pl. 23, fig. 1

1961. *Dingodinium* sp. A., Alberti : 17, pl. 3, fig. 16.

DERIVATION OF NAME. Named in honour of Dr. Gerhard Alberti, the first to describe this form of cyst.

DIAGNOSIS. A cavate dinoflagellate cyst with thin outer shell, irregularly ovoidal to subpolygonal in outline, drawn out into a blunt, stout apical horn ; inner body thin, spheroidal, with dense cover of large, pointed tubercles. Outer shell possessing clear helicoid cingulum marked by prominent folds or ridges ; further folds or ridges, less prominent, define tabulation. Intercalary archaeopyle apparently formed.

HOLOTYPE. B.M.(N.H.) slide V.51719(2). Speeton Clay, Shell West Heslerton boring at 42·50 metres depth, West Heslerton, Yorks. Lower Cretaceous (Lower Barremian).

PARATYPE. B.M.(N.H.) slide V.51723(1). Same locality and horizon.

DIMENSIONS. Holotype—overall length 66μ, breadth 52μ, length of inner body 40μ, breadth 45μ. Paratype—overall length 57μ, breadth 48μ, length of inner body 37μ, breadth 39μ. Range of dimensions—overall lengths 50–66μ, breadths 37·5–52μ.

DESCRIPTION. The outer shell is basically ovoidal to polygonal ; but it is extremely thin and is deformed in variable fashion in the seven specimens examined. It bears folds or ridges which simulate a tabulation and is drawn out into a short apical horn with a blunt, slightly rounded tip. The inner body is spheroidal and typically broader than long. The periphragm is smooth ; the endophragm smooth or very minutely granular. The latter bears a moderately dense cover of tubercles ; these are conical and do not exceed 1μ in height. There is some suggestion that the tubercles show a degree of alignment, but this could not be confirmed.

The archaeopyle is situated on the upper flanks of the epitract, in a position corresponding to the intercalary archaeopyle described by Evitt (1961*c*, text-fig. 7). The tabulation pattern was not sufficiently clear, however, to permit certainty as to whether the archaeopyle corresponded in position to an intercalary plate ; it is equally possible to visualize formation by loss of the equivalent of the anterior part only of a precingular plate.

REMARKS. Alberti (1961) recorded this form from the Lower Cretaceous (Upper Barremian) of Germany and commented that it probably constituted a new species. It occurs in the Lower Barremian horizons of the Speeton Clay (at 39 metres and 42·5 metres depth), but has not to date been encountered in the Upper Barremian.

The generic allocation is made, following Alberti, on the basis of the tuberculate structure of the inner body ; however, a tabulation is typically absent in *Dingodinium*. It was not possible to determine the plate pattern in detail, but there proved to be some similarity to the pattern exhibited in *Scriniodinium* subgenus *Endoscrinium* Klement 1960*c*, to which the species is thus possibly referable.

In the relative shapes of outer shell and inner body and in the ornamentation of the inner body ?*Dingodinium albertii* sp. nov. differs from all other described species.

Genus *PAREODINIA* Deflandre 1947 : 4

TYPE SPECIES. *Pareodinia ceratophora* Deflandre 1947. Middle Jurassic ; France.

Pareodinia ceratophora Deflandre

Pl. 23, fig. 2

1947. *Pareodinia ceratophora* Deflandre : 4, text-figs. 1–3.
1958. *Pareodinia aphelia* (para) Cookson & Eisenack : 60, pl. 12, fig. 9.
1958. *Cryptomeriapollenites coralliensis* Lantz (nom. nud.) : 927, pl. 5, figs. 55–56, pl. 6, fig. 7.
1958. Incertae sedis, Lantz : 927, pl. 6, figs. 58–59.
1960*b*. *Pareodinia ceratophora* Deflandre ; Sarjeant, pl. 12, fig. 11.
1961*a*. *Pareodinia ceratophora* Deflandre ; Sarjeant : 99, pl. 13, fig. 16.
1961. *Pareodinia ceratophora* Deflandre ; Alberti : 23, pl. 12, fig. 14.
1961. Peridinea (?) Maliavkina, Samoilovitch *et al.*, pl. 16, figs. 1, ?2.
1961. *Pareodinia* sp., Evitt, pl. 8, fig. 19.
1962*a*. *Pareodinia ceratophora* Deflandre ; Sarjeant : 263, pl. 1, fig. 13.
1962*b*. *Pareodinia certophora* Deflandre ; Sarjeant : 483, pl. 69, fig. 8 ; text-fig. 5.
1963. *Pareodinia ceratophora* Deflandre ; Balteș : 584, pl. 4, fig. 7 (mis-spelt *P. cerathophora* in text).

REMARKS. This species, first described from the Middle Jurassic, is known to occur also in the Upper Jurassic. Cookson & Eisenack (1958) embraced within their species *Pareodinia aphelia*, from the Upper Jurassic to Lower Cretaceous of Australia, what they recognized as two distinct morphological entities ; one of these (type 2) corresponds exactly with *Pareodinia ceratophora*. In the Speeton Clay, this species is represented by a handful of specimens in the Hauterivian and Barremian horizons ; in the absence of any other evidence of reworking these must be presumed to be

indigenous. *P. ceratophora* thus emerges as having a known range from Callovian to Barremian. The shape and dimensions of the Speeton specimens accord with the range quoted by Deflandre as typical (overall length 65–78μ), the figured specimen, B.M.(N.H.) slide V.51724(4), having an overall length of 71μ, with apical horn 13·5μ long, and a breadth of 57·5μ.

Genus ***SIRMIODINIUM*** Alberti 1961 : 22

TYPE SPECIES. *S. grossi* Alberti 1961. Lower Cretaceous (U. Hauterivian–U. Barremian) ; Germany.

Sirmiodinium grossi Alberti

Pl. 22, fig. 7

1961. *Sirmiodinium grossi* Alberti : 22, pl. 7, figs. 5–7, pl. 12, fig. 5.

REMARKS. This species is represented in four studied horizons of the Speeton Clay, at 39·0, 42·5, 99·25 and 103·25 metres depth. (Middle Hauterivian to Lower Barremian.) The range of dimensions exhibited is similar to, but somewhat greater than, that quoted by Alberti (overall length 87–92μ, breadth 81–85μ) ; the figured specimen, B.M.(N.H.) slide V.51722(2), having the dimensions overall length 95μ, breadth 85μ, length of inner body 65μ, breadth 63μ.

Genus ***COMETODINIUM*** Deflandre & Courteville 1939 : 98

TYPE SPECIES. *C. obscurum* Deflandre & Courteville 1939. U. Cretaceous ; France.

Cometodinium sp.

Pl. 22, fig. 6

DESCRIPTION. Shell spherical to spheroidal, minutely granular, densely covered by a mat of undulose hairlike spines. The spine-cover is lacking only in a narrow median belt corresponding to the cingulum ; this may be partly or wholly obscured from view, by the tangled spines. Archaeopyle not seen.

FIGURED SPECIMEN. B.M.(N.H.) slide V.51723(2), Speeton Clay, Shell West Heslerton Borehole at 42·5 metres depth, West Heslerton, Yorks. Lower Cretaceous (Lower Barremian).

DIMENSIONS. Figured specimen : overall length 62μ, breadth 68μ, shell length 37μ, breadth 44μ, length of spines around 15μ. Dimensions of other specimens closely similar.

REMARKS. This form has been encountered only at one horizon, in low numbers. It differs from *Cometodinium obscurum* in the lack of ridges edging the furrow ; the absence of any indication of a sulcus ; and the considerably shorter spines. It is perhaps more closely comparable to *Baltisphaeridium whitei* (Deflandre & Courteville 1939), also from the Cretaceous of France ; this latter species lacks any trace of a

cingulum, but then the cingulum is by no means easily seen in the Speeton specimens. It is therefore considered better not to propose a new name for these forms.

Genus *WETZELIELLA* Eisenack 1938c : 186

?*Wetzeliella neocomica* Gocht

1957. ?*Wetzeliella neocomica* Gocht ; 172, pl. 19, figs. 1–4, pl. 20, figs. 4, 6, 7 ; text-figs. 7, 8, 15, 16.
1961. ?*Wetzeliella neocomica* Gocht ; Alberti : 11, pl. 4, figs. 17–19.

REMARKS. This species is represented by a number of poorly preserved specimens from two horizons (Hauterivian, 99·25 and 103·25 metres depth) of the Speeton Clay ; their dimensions fall within the range quoted by Gocht (overall length 72–117μ, breadth 50–94μ) but only one specimen (B.M.(N.H.) slide V.51715(1)) is sufficiently well displayed to be measured in detail (overall length 103μ, breadth 90μ). The attribution of this species to the genus *Wetzeliella* was made with hesitation by Gocht and must be considered doubtful, since archaeopyle formation is apical and not intercalary as in typical species of that genus. However, the English specimens are too poorly preserved to be used as bases for the erection of a new genus.

It is probable that this species is related to *Muderongia*. Evitt (1961 : 397, pl. 8, figs. 1, 2) has figured as " Form G " a species from the Lower Cretaceous Dilkuna Formation of Pakistan which appears exactly intermediate between this latter genus and ?*W. neocomica*.

?*Wetzeliella neocomica* was originally recorded from the Middle Hauterivian of Germany (Gocht 1957). Alberti (1961) has recorded it from the Lower Hauterivian to Upper Barremian of Germany, from the Hauterivian of Poland and Bulgaria and from the Upper Cretaceous (Turonian and Coniacian) of Germany. The fact that it has not yet been recorded from the Aptian, Albian or Cenomanian suggests that the Upper Cretaceous specimens were reworked.

CONCLUSIONS

The known distribution of species of fossil dinoflagellate cysts in the five Speeton Clay horizons examined, is shown in the accompanying Table. A striking feature which emerges is the major change occurring in the Upper Barremian, when the incoming of seven species combines with the disappearance of seven others to change the whole character of the assemblage. The apparent change between the assemblages from 99·25 metres depth (basal Upper Hauterivian) and 42·5 metres depth (upper Lower Barremian) may be expected to fade out when intermediate assemblages are examined.

The 41 species listed in the table do not constitute the full array of dinoflagellate cysts from these five horizons ; there remains a number of species present in low numbers only and hitherto represented by damaged or obscured specimens, not capable of full description. The Speeton assemblages as a whole are remarkably rich and varied : it is clear that a number of species having a relatively limited stratigraphic range will prove of considerable value as stratigraphic indices.

TABLE 5

Horizon in the Speeton Clay of Shell West Heslerton No. 1 borehole, West Heslerton, Yorks. / Species	103·25 metres depth (Middle Hauterivian)	99·25 metres depth (Upper Hauterivian)	42·5 metres depth (Lower Barremian)	39·0 metres depth (Middle Barremian)	19·25 metres depth (Upper Barremian)
Gonyaulacysta cretacea	×	×			
G. palla			×		
G. helicoidea			×	×	
G. axicerastes				×	
G. orthoceras					
G. episoma					×
G. hadra					×
G. aichmetes					×
Heslertonia heslertonensis	×	×	×	×	×
Heliodinium patriciae	×	×			
Hystrichodinium ramoides		×			
Cribroperidinium sepimentum	×	×			
Leptodinium alectrolophum				×	
Pareodinia ceratophora		×	×	×	×
Pseudoceratium (Eopseudoceratium) gochti		×	×	×	
Gardodinium eisenacki	×	×	×		
G. albertii	×	×			
Muderongia crucis		×			
M. staurota			×		
?Wetzeliella neocomica	×	×			
Odontochitina operculata					×
?Broomea longicornuta					×
Doidyx anaphrissa			×		
Apteodinium maculatum			×		
Dingodinium albertii			×	×	
Netrelytron trinetron				×	
Paranetrelytron strongylum			×	×	
Sirmiodinium grossi	×	×	×	×	
Cometodinium sp.			×		
Fromea amphora					×
Systematophora complicata		×	×	×	
S. schindewolfi			×		
Hystrichosphaera ramosa v. ramosa				×	×
H. ramosa multibreva	×	×	×	×	×
Hystrichosphaeridium simplicispinum		×	×	×	×
H. arborispinum			×	×	
Oligosphaeridium complex		×	×	×	×
O. vasiformum	×	×	×		
O. macrotubulum	×	×			
?Cordosphaeridium fasciatum			×		
Callaiosphaeridium asymmetricum	×	×	×	×	×

Stratigraphical distribution of dinoflagellate cysts in the Speeton Clay of Shell West Heslerton No. 1 Bore.

XI. FURTHER DINOFLAGELLATE CYSTS FROM THE LONDON CLAY

By G. L. WILLIAMS & C. DOWNIE

INTRODUCTION

A number of species of dinoflagellate cysts from the London Clay have been discussed in earlier chapters. However, there remains a large residue of species also considered to be indigenous ; these are discussed in the ensuing pages. Further work on assemblages from the lower part of the London Clay of the Sheppey area and from the Thanet Sands (horizons considered to be Paleocene) is at present in progress at Sheffield by Mr. A. Husain.

Genus ***ADNATOSPHAERIDIUM*** nov.

DIAGNOSIS. Chorate cysts bearing tubular or solid intratabular processes varying in number on a single plate. Processes united distally by interconnecting trabeculae. Archeopyle apical.

TYPE SPECIES. *Adnatosphaeridium vittatum* sp. nov.

DISCUSSION. Evitt (1961*c*) suggested that, in a taxonomic subdivision of *Cannosphaeropsis* into separate genera, three factors needed to be taken into consideration : the type of archaeopyle ; the structure of the processes ; and the nature of the interconnections between processes. All these points need consideration, but the information at present available permits a subdivision into only two genera, recognized by type of archaeopyle and the position of processes with regard to plates. It is acknowledged that species now placed within *Adnatosphaeridium* represent different morphological types and that further subdivision will be necessary. *Adnatosphaeridium* includes species formerly placed in *Cannosphaeropsis*, which on account of their intratabular processes, apical archaeopyle and spherical to ellipsoidal shape, must be placed in a separate taxonomic category. When an archaeopyle is present, species of *Adnatosphaeridium* can be readily distinguished from those of *Cannosphaeropsis*.

Adnatosphaeridium vittatum sp. nov.

Pl. 24, figs. 3, 7 ; Text-fig. 56

DERIVATION OF NAME. Latin ; *vittatus*, decorated or bound with ribbons.

DIAGNOSIS. Ellipsoidal central body, with thin granular wall bearing processes of two types : slender to broadly taeniate, greatly expanded distally, and hollow open branched. Former type predominating. Adjacent processes often united distally. Reflected tabulation ?′, 6″, 5‴, 1p and 1⁗. Archaeopyle apical.

HOLOTYPE. B.M.(N.H.) slide V.51976(1). London Clay ; Sheppey, Kent, sample Sh.3.

DIMENSIONS. Holotype : diameter of central body 37μ, by 47μ, length of processes up to 20μ. Observed range : diameter of central body, width 37–66μ,

length 28 (when archaeopyle present) to 52μ; Length of processes up to 31μ. Number of specimens measured, 4.

DESCRIPTION. *Adnatosphaeridium vittatum* has strongly developed taeniate processes, often exceeding 10μ in width, which may be arranged in linear, soleate, or annular complexes. In outline, the complexes can be tubiform to flaring, distally having two orthogonal or recurved branches. The outer margin of the branches is frequently finely serrate. Branches of processes are interconnected with other processes on the same or adjacent plates. The interlinking of processes gives to them the appearance of natural arches. Some of the processes are simple and are oblate or bifid distally. Occasionally hollow branched open processes are present on the central body. Unconnected acuminate spines may arise from the processes.

OCCURRENCE. Eocene, London Clay ; Sheppey, Kent.

REMARKS. *A. vittatum* is characterized by its taeniate processes of varying width, the presence of free and united processes and the occasional hollow branched processes. The distal serrate terminations are unusual in this genus.

Adnatosphaeridium multispinosum sp. nov.

Pl. 24, fig. 5 ; Text-fig. 57

DERIVATION OF NAME. Latin ; *multus*, much, many : *spinosus*, thorny.

DIAGNOSIS. Ellipsoidal central body with thin granular endophragm. Archaeopyle apical, with zigzag margin. Periphragm forming numerous processes, slender, branched distally. Trabeculae possessing single unconnected acuminate spines.

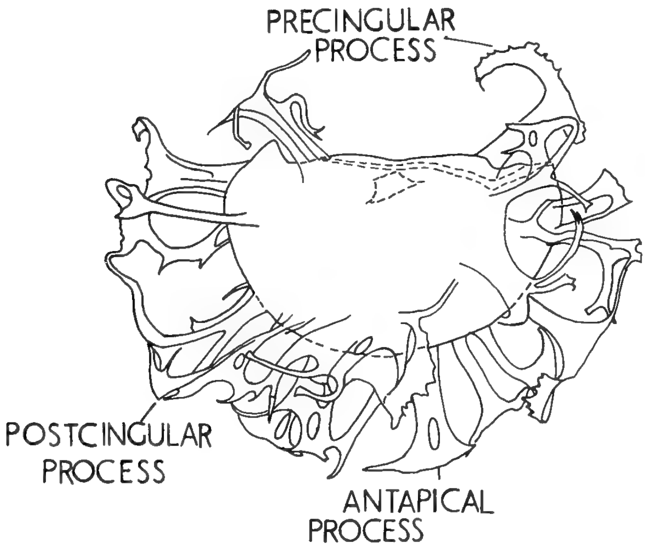


FIG. 56. *Adnatosphaeridium vittatum* sp. nov.

HOLOTYPE. B.M.(N.H.) slide V.51975(1). London Clay ; Whitecliff, sample WC 16.

DIMENSIONS. Holotype : diameter of central body 44 by 59μ. Length of processes up to 23μ. Observed range : diameter of central body 44–71μ. Length of processes up to 23μ. Number of specimens measured, 3.

DESCRIPTION. The processes of *A. multispinosum* are of approximately equal length in an individual and rarely exceed half the smaller diameter of the central body. They are erect or slightly curved, taeniate, branching from two thirds along their length to the distal extremity. The trabeculae often have short unconnected spines, sometimes arising from bulbous swellings ; the spines can be slender, up to 6μ in length or short and conical. Occasional wider processes occur. The arrangement of the processes on the central body is variable ; they can lack any regularity or be in soleate or annular complexes.

OCCURRENCE. Eocene, London Clay ; Whitecliff.

REMARKS. *A. multispinosum* differs from *A. filiferum* (= *Cannosphaeropsis filifera* Cookson & Eisenack) in possessing more numerous, generally very slender processes which can branch from two thirds along their length. *Cannosphaeropsis tutulosa* Cookson & Eisenack (1960*a*), from the Upper Cretaceous of Australia, has fewer processes which divide distally and join with neighbouring branches to form a series of relatively wide deep loops apparently lacking spines.

?***Adnatosphaeridium patulum*** sp. nov.

Pl. 24, figs. 1, 2 ; Text-fig. 58

DERIVATION OF NAME. Latin ; *patulus*, spread out, broad.

DIAGNOSIS. Sub-spherical central body with fibrous wall up to 1μ thick, composed of endocoel and pericoel. Processes intratabular open, flared, with fibrous walls ; one per plate. Adjacent processes united distally. Archaeopyle haplotabular.

HOLOTYPE. B.M.(N.H.) slide V.51977(1). London Clay ; Enborne, sample E 11.

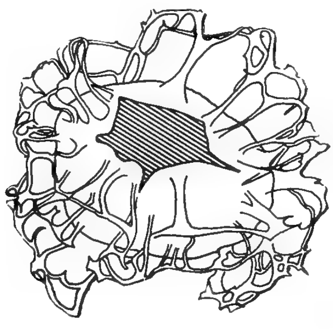


FIG. 57. *Adnatosphaeridium multispinosum* sp. nov. Holotype. Archaeopyle shaded, sulcal notch on the left.

DIMENSIONS. Holotype : diameter of central body 75 by 80μ. Length of processes up to 37μ. Observed range : diameter of central body 75–95μ. Length of processes up to 37μ. Number of specimens measured, 3.

DESCRIPTION. ?*A. patulum* has a quadrate archaeopyle resulting from the loss of a single plate. The archaeopyle is surrounded by six processes in the holotype ; these may be precingular but until more specimens are studied definite conclusions cannot be drawn. The processes are considerably broader distally than proximally and have undulose margins. Distal margins of adjacent processes are united. The fibres of the process walls are haphazard in orientation. The walls often appear perforate and this may in part be due to differential staining. The central body is medium brown, the processes tranparent, yellowish green.

OCCURRENCE. Eocene, London Clay ; Whitecliff, Enborne and Sheppey.

REMARKS. The processes readily distinguish ?*A. patulum* from other described species. Because of the uncertainty with regard to the type of archaeopyle and its shape, the species is tentatively placed in *Adnatosphaeridium*.

OTHER SPECIES

Other species occurring in the London Clay and here referred to the genus *Adnatosphaeridium* are *A. filamentosum* (Cookson & Eisenack 1958), *A. aemulum* (Deflandre 1938), *A. caulleryi* (Deflandre 1938), *A. filiferum* (Cookson & Eisenack 1958), all thought to be derived.

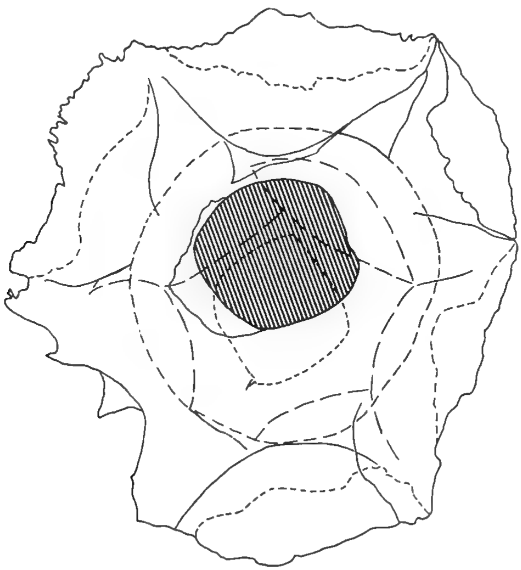


FIG. 58. *Adnatosphaeridium patulum* sp. nov. Holotype. Archaeopyle (haplotabular) is shaded.

Genus *MEMBRANILARNACIA* Eisenack 1963 : 99

EMENDED DIAGNOSIS. Chorate cysts spherical, oval or ellipsoidal, usually thick walled and surrounded by more or less concentric and generally thin walled enveloping membrane supported by processes or supports normal to central body. Processes forked, flared or branched distally. Shafts cylindrical or columnar. Archaeopyle apical.

TYPE SPECIES. *Membranilarnax leptoderma* Cookson & Eisenack 1958. Lower Cretaceous ; Papua.

DISCUSSION. Some of the species originally referred to the genus *Membranilarnax* O. Wetzel (1933) were transferred to *Membranilarnicia* by Eisenack (1963*b*). Eisenack (1959*c*) reviewed *Membranilarnax* and showed that the generic description given by O. Wetzel was ambiguous, embodying three distinct groups. These are :

1. Forms with a spherical to oval central body surrounded by a membrane restricted to the equatorial region (pterate cysts). The membrane is supported by processes arising from the central body and branching distally. A pylome (or archaeopyle) has not been observed.
2. Hystrichospheres with a spherical to oval central body surrounded by a concentric outer membrane which is supported by processes arising from the central body. A pylome (archaeopyle) can be present.
3. Hystrichospheres with a central body surrounded by a concentric outer membrane, supported by raised crests, which form polygonal fields on the central body. A pylome can be present.

To the first group can be attributed the type species of *Membranilarnax* (*M. pterospermoides* O. Wetzel). The genus should therefore be restricted to species referable to group 1, but since the structure of the holotype of *M. pterospermoides* cannot be clarified because the specimen is too deeply embedded in a flake of flint and cannot be examined at high magnification, the placing of other species within *Membranilarnax* is not to be recommended.

Eisenack (1963*b*) erected two new genera according with the second and third types. These are *Membranilarnacia* (corresponding to Group 2), and *Valensiella* (corresponding to Group 3 and synonymous with *Favilarnax* Sarjeant 1963*c* over which it has seniority). Following Eisenack's abandonment of the name *Membranilarnax*, all residual species left in that genus were provisionally transferred to *Membranilarnacia* by Downie & Sarjeant (1964). Specimens from the London Clay attributable to the genus *Membranilarnacia* possess intratabular processes indicating a reflected tabulation of 1–4′, 6″, 0–4c, 5‴, 1p, 1⁗. The archaeopyle is apical with a zigzag margin. From the tabulation and possession of intratabular processes, restricted to one per plate, *Membranilarnacia* must be included in the family Hystrichosphaeridiaceae and cannot therefore be the type genus of the family Membranilarnacidiaceae.

Membranilarnacia is distinguished from the genus *Adnatosphaeridium* by having an outer membrane instead of trabeculae, which distally unite the processes of the latter genus. It is possible however that intermediate forms exist.

Membranilarnacia reticulata sp. nov.

Pl. 24, figs. 4–6 ; Text-fig. 59

DERIVATION OF NAME. Latin, *reticulatus*, net-like, netted.

DIAGNOSIS. Ellipsoidal central body with intratabular processes, one per plate. Processes indicating a tabulation of 1–$4'$, $6''$, 4c, $5'''$, $1''''$. Cingular processes sometimes absent. Sulcal processes and posterior intercalary process present on some individuals. Processes cylindrical, solid, fibrous, united distally by a fine reticulate membrane totally or partially enclosing central body. Processes rarely exceeding 20μ in length.

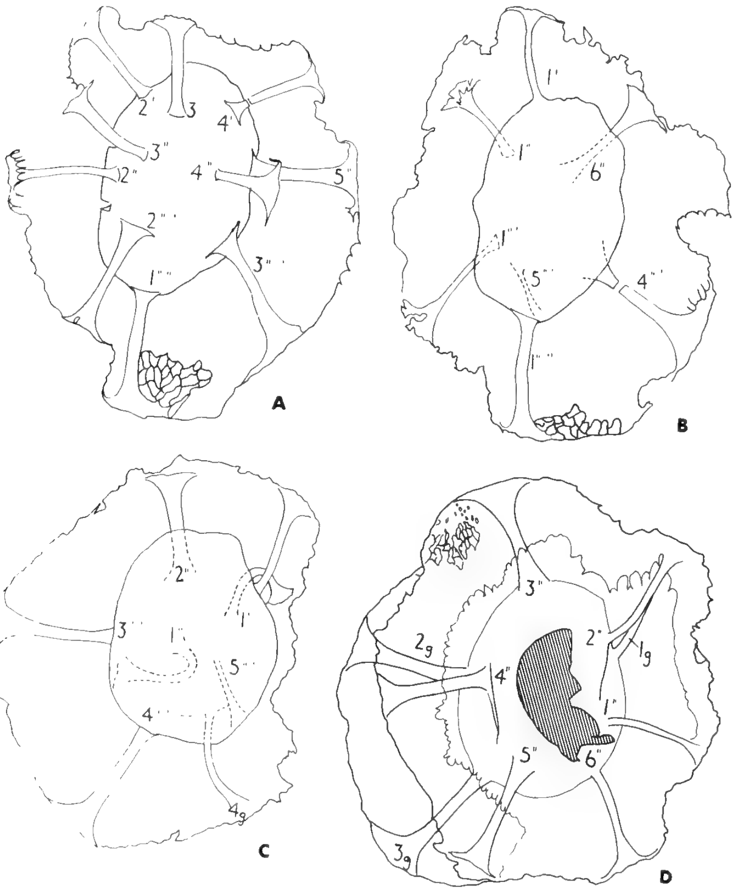


FIG. 59. *Membranilarnacia reticulata* sp. nov. A, Lower (ventral) surface, seen through the upper. Only part of the distal network uniting the processes is shown. B, Upper (dorsal) surface of same specimen. C, Lower (antapical) surface, seen through the upper. D, Upper (apical) surface of same specimen. Archaeopyle shaded, sulcal notch lies between plates $1''$ and $6''$.

HOLOTYPE. B.M.(N.H.) slide V.51959(2), London Clay ; Sheppey, Kent, sample Sh 1.

DIMENSIONS. Holotype : diameter of central body 42 by 43μ. Length of processes up to 26μ. Observed range : diameter of central body 35–44μ. Length of processes 7–24μ. Number of specimens measured, 8.

DESCRIPTION. The central body has a thin wall, smooth or slightly granular, comprising the endophragm. When an archaeopyle is present, the zigzag margin sharply delimits six rectangular plates, each bearing a process. The sulcal notch is usually clearly discernible. The process denoting the posterior intercalary plate is more commonly absent.

The fibrous processes rarely exceed two thirds of the diameter of the central body in length. They are generally simple and few in number, this being governed by the number of plates present. The size of the process may be a reflection of its position on the central body, the postcingulars often being smaller than the precingular processes. The cingulum appears to be slightly helicoidal.

The meshwork of the reticulate membrane is variable in size within an individual : it is finer nearer the process. The membrane is not unlike a closely woven net in structure, with numerous fine interconnecting orthogonal threads. The membrane may be restricted to distinct zones as in the figured specimen. There the processes of each series of plates are distally united and have few interconnecting links with processes of other plate series. This can be useful in orientation since it clarifies the position of the different plate series, and particularly the pre- and postcingulars.

Two variants of *M. reticulata* are recognized based on the arrangement of the processes. These are :

Var. *a*. Reflected tabulation as in specific diagnosis but with no cingular processes. Sulcal processes may be present. This is the commoner of the two variants.

Var. *b*. Tabulation as in specific diagnosis with cingular processes present, there being four in number.

Variability in *M. reticulata* also extends to the number of apical processes, some specimens having one, others having four. However since it is impossible to distinguish them when the archaeopyle is developed, the two forms are treated together as parts of the same species.

OCCURRENCE. London Clay ; Whitecliff, Enborne and Sheppey.

REMARKS. Comparison of *M. reticulata* with other described forms suggests close affinity with *Membranilarnax* sp. O. Wetzel (1936), from the Upper Eocene of Germany. Reissinger (1950) figured a similar form which he simply termed a " hystrichosphere ", this also being from the Eocene of Germany. Unfortunately neither of these specimens have been preserved, and only Wetzel attempted a description, brief in the extreme, stating that the form was a spiny sphere within an outer shell ; a description too succinct to be useful.

Eisenack (1954*b*) figured a specimen which he compared with *Membranilarnax* sp., O. Wetzel (1936). Eisenack (1959*c*) however inferred that the outer membrane

of *M.* sp. does not form a concentric surrounding network but is restricted to an equatorial zone, unlike that in *M. reticulata*. From the illustrations, Reissinger's form looks identical to *M. reticulata*, which often shows a conspicuous absence of the outer membrane in the equatorial zone when cingular processes are absent.

Genus ***NEMATOSPHAEROPSIS*** Deflandre & Cookson 1955 : 268

EMENDED DIAGNOSIS. Globular to ellipsoidal chorate cysts. Periphragm forms gonal or sutural processes united proximally by sutural ridges or membranes. Adjacent processes distally united by trabeculae. Archaeopyle precingular.

TYPE SPECIES. *Nematosphaeropsis balcombiana* Deflandre & Cookson, 1955. Miocene ; Australia.

DISCUSSION. The tabulation of *Nematosphaeropsis* is identical to that of *Hystrichosphaera ramosa*.

Nematosphaeropsis balcombiana Deflandre & Cookson

1955. *Nematosphaeropsis balcombiana* Deflandre & Cookson : 268, pl. 8, fig. 5.

DISCUSSION. Two specimens from the London Clay are attributed to *N. balcombiana*. They closely agree with the type material, the dimensions being : central body, length 38–40μ, breadth 28–33μ ; process length 10–22μ. The specimens were found in sample Wh 6 from Whitecliff and E 11 from Enborne.

Genus ***CANNOSPHAEROPSIS*** O. Wetzel 1932 : 140

EMENDED DIAGNOSIS. Ellipsoidal chorate cyst with precingular archaeopyle and bearing branching or furcate processes like those of *Hystrichosphaera* in both structure and distribution, but without sutural ridges or septa connecting their bases as in that genus. Processes interconnected distally by trabeculae. Endophragm and periphragm in close contact between bases of processes.

TYPE SPECIES. *Cannosphaeropsis utinensis* O. Wetzel 1932. U. Cretaceous ; Baltic.

DISCUSSION. Evitt (1963) has pointed out that many species included within *Cannosphaeropsis* (according to Deflandre's (1947) definition) significantly differ from the type species. It is therefore proposed to restrict *Cannosphaeropsis* to species possessing gonal and sutural processes allied with a precingular archaeopyle ; species with intratabular processes and apical archaeopyle, formerly attributable to *Cannosphaeropsis*, have been transferred to the genus *Adnatosphaeridium*.

No attempt is made to reallocate species of *Cannosphaeropsis* where the species in question have not been examined.

Cannosphaeropsis reticulensis Pastiels

Pl. 24, fig. 8

1948. *Cannosphaeropsis reticulensis* Pastiels : 49, pl. 5, figs. 7–10.
1961. *Cannosphaeropsis reticulensis* Pastiels ; Alberti : 36, pl. 9, fig. 15.

Discussion. Specimens of *C. reticulensis* possessing a precingular archaeopyle with gonal and sutural processes, are present in the London Clay. The interconnecting trabeculae appear to be solid, taeniate and not tubular. The simple acuminate spines arising from the trabeculae of the type material are uncommon in the London Clay forms.

Dimensions. Range observed in London Clay : diameter of central body 26–43μ, length of processes 9–18μ. Number of specimens measured, 5.

Occurrence. Eocene, London Clay ; Whitecliff, Enborne and Sheppey. *C. reticulensis* is also known from the Eocene of Belgium (Pastiels 1948) and Germany (Alberti 1961).

Genus *CYCLONEPHELIUM* Deflandre & Cookson 1955 : 285

Emended diagnosis. Chorate cysts with central body flattened dorso-ventrally and apparently concavo-convex, outline circular to slightly oval. Apex and/or antapex with or without blunt prominence, antapex occasionally slightly indented. Ornamentation restricted to circumferential zone of varying width, consisting of (1) processes, of varying lengths and shapes, distinct or more or less confluent, (2) thin membrane supported at intervals by strong processes, or (3) densely arranged surface thickenings. Ornamentation sometimes more strongly developed in antapical region. Archaeopyle apical tetrabular. Wall layers not distinguished.

Type species. *Cyclonephelium compactum* Deflandre & Cookson 1955. Lower to Upper Cretaceous ; Australia.

Discussion. Tabulation cannot be determined in this genus beyond the fact that there are four apical and six precingular plates. This is apparent from an examination of a detached operculum and the margin of the archaeopyle, which is zigzag.

The shape of specimens of *Cyclonephelium* is variable and is probably partly dependent on subsequent compression in the enclosing sediment. Individuals of the species *C. exuberans* Deflandre & Cookson 1955, are often similar to *Areoligera* in having a convex dorsal surface and a depressed ventral surface. This is not, however, universal, since others appear to have an ellipsoidal outline, both dorsal and ventral surfaces being convex.

Cyclonephelium divaricatum sp. nov.

Pl. 25, fig. 1 ; Text-fig. 60

Derivation of name. Latin ; *divaricatus*, spread apart.

Diagnosis. Central body flat or slightly convex with circular outline bearing numerous ambital taeniate processes. Processes united distally in complex

fashion, sometimes by trabeculae, sometimes by perforated membranes. Erect unconnected secae, acuminate or bifid distally, arising from outer margin of trabeculae or membranes. Length of processes rarely exceeding one-third the diameter of the central body.

HOLOTYPE. B.M.(N.H.) slide V.51956(2). London Clay ; Whitecliff, sample 8.

DIMENSIONS. Holotype : diameter of central body 54 by 71μ. Observed range : diameter of central body 45–71μ. Length of processes up to 15μ. Number of specimens measured, 5.

DESCRIPTION. The central body has a finely reticulate surface and is formed from the extremely thin endophragm. The periphragm gives rise to the taeniate processes. The numerous processes are restricted to the ambitus of the central body save on the precingulars, where the processes surround the archaeopyle margin. The processes are short, with only a few distal interconnctions. They tend to exhibit a linear orientation and are often united proximally. The secae, arising from the distal margin of the trabeculae or membranes that unite the processes, often appear to be continuations of the processes distally, whilst at other times they arise at points distant from the processes. Occasional simple acuminate processes are present on the central body.

OCCURRENCE. Eocene, London Clay ; Whitecliff, Enborne, Sheppey and Studland.

REMARKS. *C. divaricatum* differs from other described species of *Cyclonephelium* in the nature of the processes distally and the point of origin of the trabeculae or interconnecting membrane.

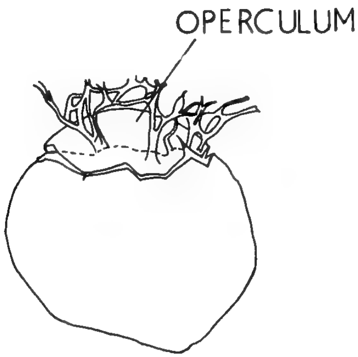


FIG. 60. *Cyclonephelium divaricatum* sp. nov. Partial drawing of specimen showing operculum separating from the test.

Cyclonephelium exuberans Deflandre & Cookson

Text-fig. 61

1948. *Membranilarnax pterospermoides* Pastiels : 46, pl. 5, figs. 11–14.
1955. *Cyclonephelium exuberans* Deflandre & Cookson : 281.

DISCUSSION. *C. exuberans* has probably evolved from *C. pastielsi*, intermediate forms between the two being common. Specimens from the London Clay show the same variation in process distribution as *C. pastielsi*, some individuals lacking processes on plates 3″ and 6″, others having processes on all the precingular plates, although generally with fewer on 3″ and 6″ than on the others. The prominent sulcal notch lies to the right of the mid-ventral line. The surface of the central body is commonly granular.

DIMENSIONS. Range observed in London Clay : diameter of central body 56–85μ, length of processes up to 46μ. Number of specimens measured, 4.

OCCURRENCE. Eocene, London Clay ; Whitecliff and Enborne ; Eocene (Ypresian) of Belgium (Pastiels 1948).

Cyclonephelium ordinatum sp. nov.

Pl. 25, fig. 3 ; Text-fig. 62

DERIVATION OF NAME. Latin ; *ordinatus*, in row, orderly.

DIAGNOSIS. Thin walled central body with granular surface. Processes formed from periphragm and restricted to linear complexes regularly distributed on central

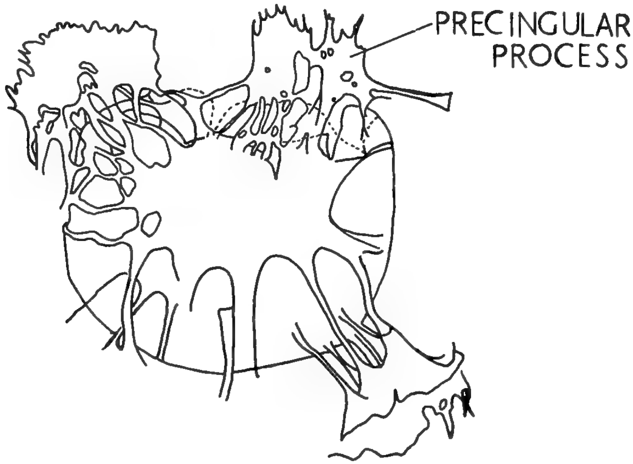


FIG. 61. *Cyclonephelium exuberans* (Pastiels). Partial drawing showing large precingular processes around the margin of the archaeopyle (broken line).

body. Reflected tabulation deduced from linear complexes of 4′, 6″, 5‴, 1p, 1⁗. Processes slender, solid, taeniate, united half to two-thirds along their length by membranes or trabeculae. Processes distally unconnected and unequally bifurcate.

HOLOTYPE. B.M.(N.H.) slide V.51977(2). London Clay ; Enborne, Borehole E 11, 61 ft.

DIMENSIONS. Holotype : diameter of central body 61 by 73μ. Length of processes up to 36μ. Observed range : diameter of central body 41–74μ, length of processes up to 40μ. Number of specimens measured, 4.

DESCRIPTION. This species is unusual in that it possesses processes restricted to the ambitus yet which are grouped into linear or sometimes arcuate complexes reflecting a dinoflagellate tabulation. The apical archaeopyle is nearly always developed and had a clear sulcal notch. The precingulars possess a variable number of processes, plates 1″, 2″, 4″ and 5″ having well-developed linear complexes, 3″ having a complex of varying extent, whilst 6″ can be devoid of processes.

The processes are not unlike those of *Areoligera medusettiformis* (O. Wetzel). The interconnecting membrane sometimes extends to the base of the processes and, if so developed, is often fenestrate proximally. Distally the processes are bifurcate commonly with one fork longer than the other and recurved. Occasionally the processes are acuminate. Branching can occur distally to the interconnecting membrane or trabeculae.

OCCURRENCE. Eocene, London Clay ; Whitecliff and Enborne.

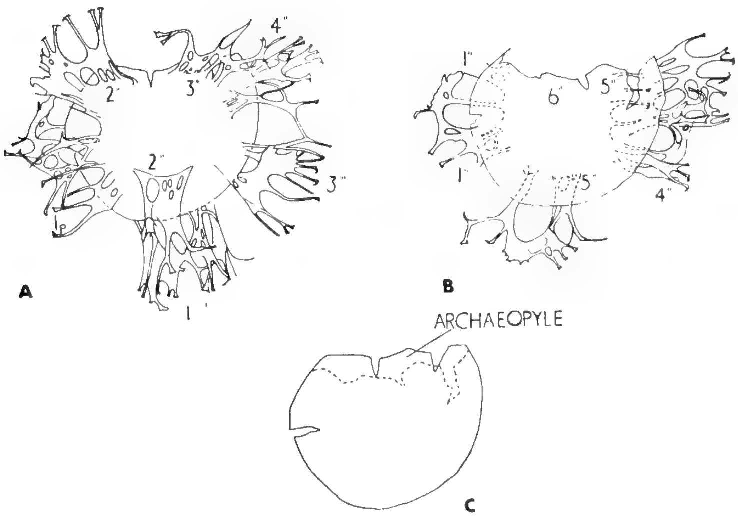


FIG. 62. *Cyclonephelium ordinatum* sp. nov. Holotype. A, Tabulation of the upper (dorsal) surface. B, Tabulation of the lower (ventral) surface seen through the upper. C, Partial drawing to show the ziz-zag nature of the archaeopyle margin.

REMARKS. *C. ordinum* differs from *C. divaricum* in the regular arrangement of the processes in linear complexes and the larger overall size. It is included within the genus *Cyclonephelium* on account of the absence of processes from the mid-dorsal and ventral surface apart from those on the margin of the archaeopyle.

Cyclonephelium pastielsi Deflandre & Cookson

Pl. 25, fig. 2

1948. *Membranilarnax* cf. *liradiscoides* Pastiels : 47, pl. 5, fig. 15.
1955. *Cyclonephelium pastielsi* Deflandre & Cookson : 285.

DISCUSSION. Specimens of *C. pastielsi* from the London Clay almost invariably possess an archaeopyle, apical in position and with a zigzag margin. The prominent sulcal notch lies to the right of the mid-ventral line. Only rarely is a complete individual, with the apex in place, encountered. The numerous, solid taeniate processes are complexly united along their length and distally. They are frequently arranged in linear complexes. Proximally the processes arise singly or in groups of twos or threes. Distally the interconnecting trabeculae may be perforate, up to 5 to 6μ in width. Unconnected short, slender, acuminate or bifid spines often arise from the trabeculae. Occasional simple acuminate processes occur on the central body.

Pastiels figured a specimen of *C. pastielsi* (as *Membranilarnax* cf. *liradiscoides*, pl. 5, fig. 15) showing an absence of processes round the mid-ventral and mid-dorsal margins of the archaeopyle. In the majority of the London Clay forms the processes are rather more numerous on the ambitus and also completely surround the archaeopyle margin. Those processes round the archaeopyle are more complex in structure than the ambital processes, and are aligned in rows parallel to the margin of the archeopyle. It is probable that each precingular and postcingular plate has processes to a greater or lesser degree.

Specimens of *C. pastielsi* can have two antapical protuberances, one more strongly developed than the other. When these are present the outline of the central body is closely comparable to that of *Areoligera*. The size of the London Clay forms usually exceeds that of the type material. Transitional forms to *C. exuberans* are not uncommon.

DIMENSIONS. Observed range in London Clay : diameter of central body 43–90μ, length of processes 12–38μ. Number of specimens measured, 25.

OCCURRENCE. Common at all horizons of the London Clay. The forms having the larger central bodies are commonest in WC.14, 26 and E.11/88. *C. pastielsi* has also been recorded from the Ypresian of Belgium (Pastiels 1948).

Genus ***AREOLIGERA*** Lejeune-Carpentier 1938 : 164

EMENDED DIAGNOSIS. Chorate cysts with hemispheral central body, convex dorsal side and flat or depressed ventral side. Processes intratabular, on dorsal surface arranged in soleate or annular complexes, on ventral surface in linear or

occasionally soleate complexes. Plate 1'''' possesses an annular complex. Cingulum indicated by reduced linear complexes Reflected tabulation of 4', 6'', 2–4c, 5''', 1p, 1''''. Archaeopyle apical tetratabular. Well developed sulcal notch on ventral surface and lying to right of mid-ventral line. Outline of central body circular with bilobed antapex.

TYPE SPECIES. *Areoligera senonensis* Lejeune-Carpentier 1938*b*. Upper Cretaceous (Senonian) ; Belgium.

DISCUSSION. Evitt (1961, 1963) has given a full and concise review of the genus. The close relationship to certain species of *Cyclonephelium* has been noted in preceding pages.

Areoligera coronata (O. Wetzel)

Pl. 25, fig. 7

1933. *Hystrichosphaera penicillata* forma *coronata* O. Wetzel : 41, pl. 4, fig. 17.
1938. *Areoligera coronata* (O. Wetzel) Lejeune-Carpentier : 168, text-fig. 6.

DISCUSSION. *A. coronata* in the Eocene exhibits considerable variation in the structure of the soleate complexes. Proximally these can be fenestrate or non-fenestrate membranes, with the processes arising from the distal margin of the membrane. Alternatively, the processes may arise directly from the central body and be united along their length by membranes. Distally the slender processes are erect and can be acuminate or bifid. The number of processes per complex is variable Not infrequently plates 2''' and 4''' have annular and not soleate complexes ; if this is the case, the processes nearest the transverse cingulum are usually shorter. In one individual the processes of adjacent complexes are united distally by trabeculae.

Only plate 6'' never has processes. The apical plates possess four process groups, the smallest of which is that on plate 1'. This is a single taeniate process branched distally. Plates 2' and 3' have tubular annular complexes, diversely branched distally ; these give the impression of having developed from a simple tubular process. Plate 4' has a taeniate process which is branched distally and is intermediate in size between process 1' and processes 2' and 3'.

DIMENSIONS. Range observed in London Clay : diameter of central body, length 53–66μ, breadth 57–76μ ; length of processes 10–38μ. Number of specimens measured, 5.

OCCURRENCE. Eocene, London Clay ; Whitecliff and Sheppey ; Upper Cretaceous of Germany (O. Wetzel 1933).

Areoligera cf. ***coronata*** (O. Wetzel)

Pl. 25, fig. 5 ; Text-fig. 63

DESCRIPTION. Included here are three specimens which differ from *A. coronata* in having process complexes on all the plates, 6'' having a soleate complex, whilst

plates 1‴ and 5‴ bear multibranched linear or annular complexes. There are at least four cingular plates and some sulcal plates having linear complexes. The dorsal surface is convex, the ventral surface depressed. The processes on the ventral surface are closer to those of *A. medusettiformis* than those of *A. coronata*, and can be simple or branched distally or proximally.

A. cf. *coronata* resembles *Systematophora* in having process complexes on both ventral and dorsal surfaces. In the shape of the central body, position of the sulcal notch and predominance of soleate complexes however, it more closely approximates to *Areoligera* with which genus it must be included.

DIMENSIONS. Observed range : diameter of central body 57–71μ, length of processes up to 27μ.

OCCURRENCE. Eocene, London Clay ; Sheppey, Kent.

Areoligera cf. ***medusettiformis*** (O. Wetzel)

Pl. 25, fig. 4

DESCRIPTION. This has similar processes to *A. medusettiformis* and the same shape of central body. It differs, however, in the presence of process complexes on all the fields and not on the dorsal fields only. The precingular plates bear soleate complexes, whilst plates 1‴ and 5‴ have annular complexes. The complexes are unusual in being formed partly from simple processes, especially is this so with those processes nearest to the mid-ventral line. There is a well developed right antapical protuberance which is almost in line with the sulcal notch.

DIMENSIONS. Observed range : diameter of central body, 50–67μ, length of processes up to 3μ. Number of specimens measured, 2.

OCCURRENCE. Eocene, London Clay ; Sheppey, Kent.

FIG. 63. *Areoligera* cf. *coronata* (O. Wetzel). Left, upper (ventral) surface ; right, lower (dorsal) surface, viewed through upper. Archaeopyle shaded. GP, girdle processes ; PS, posterior sulcal processes.

Areoligera cf. ***senonensis*** Lejeune-Carpentier
Pl. 25, fig. 6 ; Text-fig. 64

Description. One beautifully preserved individual from the London Clay of Sheppey, whilst having the distinctive processes of *A. senonensis*, also possesses process complexes on the ventral surface. The excellent preservation enabled the tabulation of 6″, 5‴, 1p, 1⁗ to be determined. The six precingulars bear soleate process complexes, four of the postcingulars, 1‴, 2‴, 4‴ and 5‴ bear annular complexes. The single antapical protuberance lies immediately beneath the sulcal notch.

A single archaeopyle operculum possessing four annular complexes can also be attributed to *A.* cf. *senonensis*. This has an elongate plate 1′, with plates 2′ and 3′ considerably larger than the other two plates.

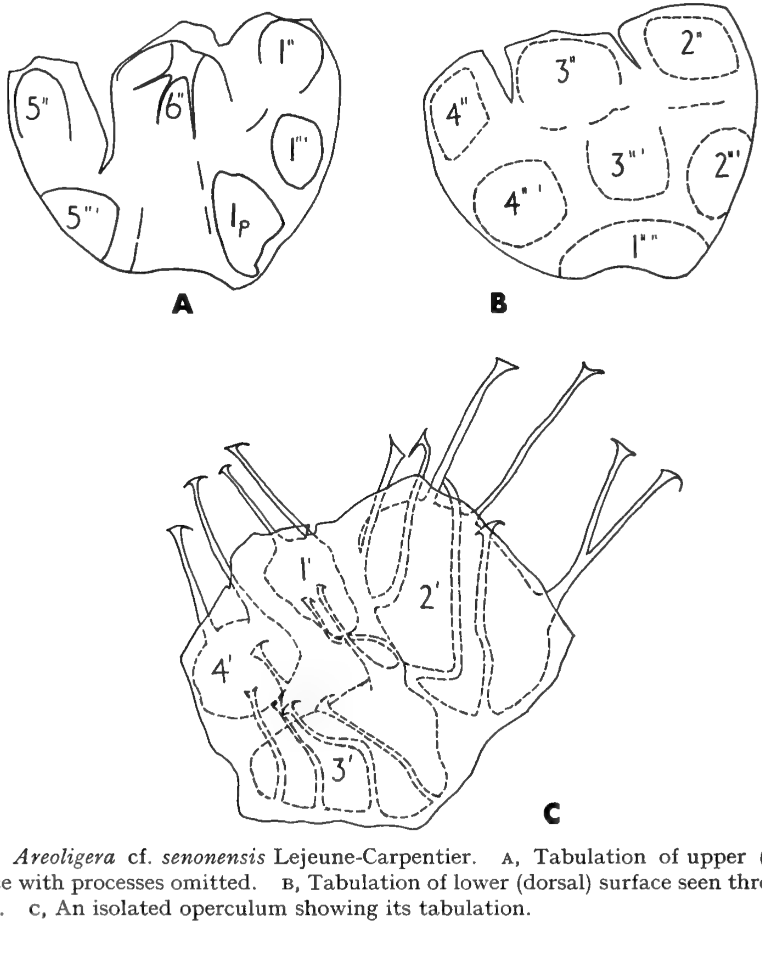


Fig. 64. *Areoligera* cf. *senonensis* Lejeune-Carpentier. A, Tabulation of upper (ventral) surface with processes omitted. B, Tabulation of lower (dorsal) surface seen through the upper. C, An isolated operculum showing its tabulation.

DIMENSIONS. Diameter of central body 70 by 85μ. Length of processes up to 28μ.

OCCURRENCE. Eocene, London Clay ; Sheppey, Kent.

REMARKS. *A.* cf. *senonensis*, like *A.* cf. *medusettiformis* and *A* cf. *coronata* is a form approaching the genus *Systematophora*. The London Clay forms attributed to *Areoligera*, differ from *Systematophora* only because of the presence of process complexes on the central surface, in particular on plate 6″ which is usually barren of processes.

Genus ***DEFLANDREA*** Eisenack 1938 : 187

EMENDED DIAGNOSIS. Cavate cysts with periphragm forming elongate pentagonal (also often somewhat rounded to rhomboidal) outer shell. Lateral walls usually convex. One apical and two antapical horns, more or less reduced. Tabulation, when decipherable, peridinoid. Periphragm smooth or granular. Cingulum circular longitudinal furrow if observable restricted to hypotract. Inner capsule circular to ovoidal in outline ; endophragm of variable thickness. Archaeopyle intercalary.

TYPE SPECIES. *D. phosphoritica* Eisenack 1938. Oligocene ; East Prussia.

DISCUSSION. The genus *Deflandrea* is represented by a large number of species, some of which clearly overlap. To avoid further confusion, many specimens figured are not given a specific name or detailed description since slight changes in outline of the pericoel are not considered worthy of specific differentation.

Deflandrea phosphoritica subsp. ***phosphoritica*** Cookson & Eisenack

Pl. 26, figs. 2, 3, 6, 9

1961*b*. *Deflandrea phosphoritica* subsp. *phosphoritica* Cookson & Eisenack : 39.

DISCUSSION. This subspecies, common in the London Clay, often possesses a clearly marked indented circular cingulum and a sulcus restricted to the hypotract and widening posteriorly. The outline of the periphragm varies from being identical to the type material to closely approaching *Deflandrea phosphoritica* subsp. *australis* Cookson & Eisenack 1961, which has a more granular periphragm and a short solid cylindrical process at the distal extremity of the apical horn and frequently more pronounced antapical horns.

A few specimens without a capsule were observed ; in one the interior was empty, in the others formless organic matter appeared to have formed from decay of the capsule.

The archaeopyle of the London Clay specimens of *D. phosphoritica* subsp. *phosphoritica* is always intercalary in the periphragm but appears to occupy a more apical position in the endophragm. The granules on the surface of the periphragm often delimit plate boundaries and also tend to show linear alignment, running from the apex towards the antapex.

DIMENSIONS. Observed range in London Clay : outer shell, length 110–133μ, breadth 75–103μ ; capsule, length 55–75μ, breadth 66–86μ. Number of specimens measured, 13.

OCCURRENCE. Eocene, London Clay ; Whitecliff, Enborne, Sheppey and Studland. Also from the Palaeocene to the Oligocene in Europe and the Lower Tertiary of Australia.

Deflandrea phosphoritica subsp. ***australis*** Cookson & Eisenack

Pl. 26, fig. 4

1961*b*. *Deflandrea phosphoritca* subsp. *australis* Cookson & Eisenack, pl. 1, figs. 2, 3.

DISCUSSION. Only three specimens from the London Clay can be definitely attributed to *D. phosphoritica* subsp. *australis*, although intermediate forms to *D. phosphoritica* subsp. *phosphoritica* are common.

DIMENSIONS. Observed range in London Clay : outer shell, length 138–157μ, breadth 72–104μ, capsule, length 69–75μ, breadth 52·6–87μ.

OCCURRENCE. Eocene, London Clay ; Enborne and Sheppey. Also occurs in the Lower Tertiary of Australia (Cookson & Eisenack 1961*b*).

Deflandrea denticulata Alberti

1948. *Peridinium* cf. *galeatum* (pars.) Pastiels : 50, pl. 5, figs. 17–20.
1959. *Deflandrea denticulata* Alberti ; 102, text-fig. 1.

DISCUSSION. The London Clay specimens attributable to *D. denticulata* are generally smaller than the type material and are sufficiently well preserved to give details of tabulation, determinable from the small acuminate or blunt processes that occasionally delimit the plate boundaries. These indicate the presence of four apical, three anterior intercalary, five postcingular, and as yet unknown numbers of precingular and antapical plates. The archaeopyle is intercalary, resulting from the loss of plate 2a. The tabulation of *D. denticulata* is thus peridinoid. The small processes, often longer on the prominent apical and antapical horns, are not restricted to the plate boundaries. They have a tendency to be orientated in linear complexes running in an antero-posterior direction. The sutures of the indented sulcus are always denticulate.

DIMENSIONS. Range in London Clay : outer shell, length 72–126·5μ, breadth 43–74μ ; capsule, length 37–64μ ; breadth 38–61μ, length of apical horn 20–39μ. Number of specimens measured, 15.

OCCURRENCE. Eocene, London Clay ; Whitecliff, Enborne and Sheppey. Also recorded from the Palaeocene to the Lower Eocene in Germany (Alberti 1959*b*), and from the Ypresian in Belgium (Pastiels 1948).

Deflandrea oebisfeldensis Alberti

Pl. 26, fig. 1

1959*b*. *Deflandrea oebisfeldensis* Alberti : 95. pl. 8, figs. 10–13.

DISCUSSION. Two specimens from the London Clay are positively identified as *D. oebisfeldensis* ; one of them does not possess a capsule.

OCCURRENCE. Eocene, London Clay ; Enborne and Sheppey. Recorded also from the Palaeocene to the Lower Eocene in Germany and from Stalingrad, Russia (Alberti 1959*b*).

Deflandrea wardenensis sp. nov.

Pl. 26, fig. 5

DERIVATION OF NAME. From Warden Point, Sheppey, Kent.

DIAGNOSIS. Cavate cysts, sub-circular to ovoidal periphragm, one apical and two short antapical horns. Conical apical horn merging imperceptibly into lateral walls; two antapical horns more positively delimited and straight or slightly diverging Length of antapical horns approximately equal. Thin walled ovoidal capsule, closely appressed to periphragm except at horns. Surface of periphragm has short acuminate or blunt processes, not restricted to sutures of cingulum and sulcus. Archaeopyle common.

HOLOTYPE. B.M.(N.H.) slide V.51980(1). London Clay ; Sheppey, Kent. sample 2.

DIMENSIONS. Holotype : periphragm, length 57μ, breadth 46μ ; capsule, length 36μ, breadth 43μ. Observed range : periphragm, length 46–64μ, breadth 43–50μ, capsule, length 33–41μ, breadth 40–46μ. Number of specimens measured, 6.

DESCRIPTION. The epitract is longer than the hypotract. In outline the former is conical with convex lateral sides, the latter is rounded with the antapical horns being sharply delimited. All three horns can be acuminate but are more commonly blunt. The antapical horns are well separated. The equatorial and longitudinal furrows are both wide with the latter broadening posteriorly. Five postcingulars have been discerned ; the rest of the tabulation is too difficult to decipher.

OCCURRENCE. Eocene, London Clay ; Sheppey, Whitecliff and Enborne.

REMARKS. Species of *Deflandrea* having processes on the sutures of the cingulum, sulcus and plate boundaries are *D. denticulata* ; *D. echinoidea* Cookson & Eisenack 1958 (Upper Cretaceous ; Australia) ; and *D. spinulosa* Alberti 1959 (Oligocene ; Germany). All these have distinctive outlines which readily distinguish them from *D. wardenensis*.

Genus ***THALASSIPHORA*** Eisenack & Gocht 1960 : 51

Emended diagnosis. Pterate cysts with spherical to ellipsoidal central body, smooth or more commonly granular. Periphragm in form of helmet-shaped " lamellar wing " and in contact with endophragm only on dorsal surface of central body. Archaeopyle precingular.

Type species. *Bion pelagicum* Eisenack 1938. Oligocene ; East Prussia.

Discussion. *Thalassiphora* Eisenack & Gocht is now considered to be referable to the Dinophyceae (Downie, Evitt & Sarjeant 1963) on account of the frequently occurring archaeopyle. As Alberti (1961) noted, the structure of *Thalassiphora* resembles that of *Pterospermopsis* superficially but detailed examination shows that in the former, the periphragm is attached to the endophragm on one surface of the central body only, the dorsal surface. The periphragm extends considerably beyond the central body as a wing lamella, in shape resembling an inverted basin with the margin often turned over. The position of the archaeopyle is constantly dorsal anterior, the keel when present, is posterior. If an archaeopyle is present, it occurs in the periphragm and endophragm. Free opercula are often encountered in sample.

In *Pterospermopsis*, the wing lamella is in contact with the central body along an " equatorial zone " only. Species of *Pterospermopsis* do not possess an archaeopyle.

Thalassiphora pelagica (Eisenack)

Pl. 26, fig. 7

1938. *Bion pelagicum* Eisenack : 187.
1954. *Pterospermopsis pelagica* (Eisenack) Eisenack : 71, pl. 12, figs. 17, 18.
1960. *Thalassiphora pelagica* (Eisenack) Eisenack & Gocht : 513, text-figs. 1–3.
1961. *Pterospermopsis pelagica* (Eisenack) ; Gerlach : 209, pl. 28, fig. 15.
1963. *Thalassiphora pelagica* (Eisenack) ; Gerlach : 50, pl. 3, fig. 3.
1963. *Thalassiphora pelagica* (Eisenack) ; Brosius : 50, pl. 3, fig. 3.

Discussion. *T. pelagica* is characterized by the presence of a keel on the periphragm. In the London Clay, orientation of the specimens has been guided by the position of the archaeopyle, which forms by the loss of a single precingular plate. The archaeopyle is anterior in position, the keel always being posterior with respect to this. The face of the central body containing the archaeopyle is dorsal. The archaeopyle is present in the periphragm and endophragm and has a convex triangular outline. Specimens with the operculum lying within the central body have been observed. The ovoidal central body has a wall up to 1·5μ thick. The thick periphragm is fibrous with a reticulate ornamentation ; it can be perforate. In size, the London Clay forms show close agreement with the type material.

Dimensions. Range observed in London Clay ; overall diameter 170–220μ ; central body 85–107μ ; archaeopyle 30–42μ ; keel 13μ. Number of specimens measured, 6.

Occurrence. Eocene, London Clay ; Sheppey, Kent, and from the Upper Eocene to Middle Miocene of Germany.

Thalassiphora delicata sp. nov.

Pl. 26, fig. 8

Derivation of name. Latin ; *delicatus*, tender, dainty.

Diagnosis. A *Thalassiphora* with ellipsoidal central body possessing a smooth thin wall. Periphragm in form of wing lamella, delicate, often irregularly folded and turned over on its margin. No keel present. Periphragm can be perforate. An archaeopyle may be present.

Holotype. B.M.(N.H.) slide V.51756(3). London Clay ; Enborne, sample E 11.

Dimensions. Holotype : diameter of central body 34 by 43μ, overall diameter 74 by 75μ. Observed range : diameter of central body 34–57μ, overall diameter 74–120μ. Number of specimens measured, 4.

Description. *T. delicata* exhibits considerable variation in width of the periphragm, this is partly due to unequal folding. Some of the folds on the periphragm suggest the presence of a cingulum ; this is however difficult to visualise since the periphragm does not completely surround the central body. Both the endophragm and periphragm are thin.

Remarks. This is only the third species allocated to this genus. It differs from the other two in size, the extremely thin periphragm and endophragm, the commonly perforate periphragm and the absence of a keel.

XII. ACKNOWLEDGMENTS

The authors have received help from many specialists in varying degree and would like to express their thanks for the ready and full co-operation afforded them. In particular they would like to thank Prof. Georges Deflandre, for much help and for courtesy in entertaining two of the authors (R.J.D. and W.A.S.S.) and allowing them to examine holotypes at the Laboratoire de Micropaléontologie, Ecole Pratique des Hautes Etudes, Paris ; Prof. A. Eisenack and Herr Hans Gocht, for their courtesy in entertaining two of the authors (C.D. and W.A.S.S.) and permitting study of holotypes in the collections of the Geologisches Institut, University of Tübingen ; Dr. W. R. Evitt, of Stanford University, California, for much assistance in the formulation of the concepts here expressed ; Dr. J. W. Neale, of the University of Hull, and Dr. P. Kaye, of Burmah Oil Co., for their advice on Speeton Clay stratigraphy ; Mr. D. Curry for his advice on London Clay stratigraphy ; Dr. G. Norris, of McMastter University, Hamilton, Ontario, for profitable discussions, particularly on *Gonyaulacysta* and allied forms ; Dr. K. Diebel, of the Institut für Paläontologie, Humboldt University, Berlin, for courteously permitting the loan, for study, of Ehrenberg's holotypes ; and Professors W. D. Evans and L. R. Moore, of the Universities of Nottingham and Sheffield, for their help and encouragement.

They would further like to acknowledge the courtesy of Shell Internationale Research Maatschappij J.V., the Hague, Netherlands, for permitting study of Speeton Clay specimens from the West Heslerton No. 1 Borehole and for permitting

publication of the relevant parts of this paper ; Professor H. L. Hawkins for making the Enborne Borehole cores available, and Sir James Stubblefield of H.M. Geological Survey, for permitting study of chalk specimens from the Fetcham Mill Borehole, and for permitting publication of the relevant parts of the paper.

Finally, the assistance of Mrs. P. E. Lunn, Miss Eileen Bruce and Miss Denise Hales in the preparation of the manuscript, and of Mr. J. Eyett in photography, is gratefully acknowledged.

The work of two of the authors (R.J.D. and G.L.W.) was done under the tenure of D.S.I.R. research studentships.

XIII. REFERENCES

ALBERTI, G. 1959. Zur Kenntnis der Gattung *Deflandrea* Eisenack (Dinoflag.) in der Kreide und im Alttertiär Nord und Mitteldeutschlands. *Mitt. Geol. Staatsinst. Hamburg*, **28** : 93–105, pls. 8, 9.

—— 1961. Zur Kenntniäs mesozoischer und alttertiär Dinoflagellaten und Hystrichosphaerideen von Nord—und Mitteldeutschland sowie einigen anderen europäischen Gebieten. *Palaeontographica*, Stuttgart (A) **116** : 1–58, pls. 1–12.

BALTES, N. 1963. Dinoflagellate și Hystrichosphaeride ćretacice din Platforma moezică. *Petrol și Gaze*, Bucurest, **14** : 581–597, pls. 1–8.

—— 1965. Observații asupra microflorei ćretacice inferioaredin zona R. Bicaz. *Petrol si Gaze*, Bucurest, **16** : 3–17, pls. 1–4.

BRONN, H. G. 1848. Handbuch einer Geschichte der Natur. *Index palaeontologicus.* 1382 pp. Stuttgart.

BROSIUS, M. 1963. Plankton aus dem nordhessischen Kasseler Meeressand (Oberoligozän). *Z. deutsch. Geol. Ges.*, Berlin, **114** : 32–56, pls. 1–8.

CONRAD, W. I. 1941. Notes protistologiques XIX. Quelques microfossiles des siles crétacés. *Bull. Mus. roy. Hist. Nat. Belg.*, Bruxelles, **17** : 1–10, pl. 1.

COOKSON, I. C. 1953. Records of the occurrence of *Botryococcus braunii*, *Pediastrum* and the Hystrichosphaeridae in Cainozoic deposits of Australia. *Mem. Nat. Mus. Melbourne*, **18** : 107–123, pls. 1, 2.

—— 1956. Additional Microplankton from Australian Late Mesozoic and Tertiary sediments. *Aust. J. Mar. Freshwater Res.*, Melbourne, **7** : 183–191, pls. 1, 2.

—— 1965. Cretaceous and Tertiary Microplankton from South-eastern Australia. *Proc. Roy. Soc. Victoria*, Melbourne, **78** : 85–93, pls. 9–11.

COOKSON, I. C. & EISENACK, A. 1958. Microplankton from Australian and New Guinea Upper Mesozoic sediments. *Proc. Roy. Soc. Victoria*, Melbourne, **70** : 19–79, pls. 1–12.

—— 1960*a*. Microplankton from Australian Cretaceous sediments. *Micropaleontology*, New York, **6** : 1–18, pls. 1–3.

—— 1960*b*. Upper Mesozoic microplankton from Australia and New Guinea. *Palaeontology*, London, **2** : 243–61, pls. 37–39.

—— 1961*a*. Upper Cretaceous microplankton from the Belfast no. 4 bore, South-Western. Australia. *Proc. Roy. Soc. Victoria*, Melbourne, **74** : 69–76, pls. 11, 12.

—— 1961*b*. Tertiary microplankton from the Rottnest Island bore, Western Australia. *J Proc. Roy. Soc. W. Aust.*, Perth, **44** : 39–47, pls. 1, 2.

—— 1962. Additional microplankton from Australian Cretaceous sediments. *Micropaleontology*, New York, **8** : 485–507, pls. 1–7.

COOKSON, I. C. & HUGHES, N. F. Microplankton from the Cambridge Greensand (mid-Cretaceous). *Palaeontology*, London, **7** : 37–59, pls. 5–11.

CURRY, D. 1958. Hystrichosphaeridae from the English Eocene. List of Exhibits, Annual Reports. *Proc. Geol. Ass., Lond.*, **69** : 56.

—— 1958*a*. *Geologist Association Guide No. 25. The Isle of Wight II. The Tertiary* : 11–19, 1 fig.

DAVIS, A. G. 1936. The London Clay of Sheppey and the location of its fossils. *Proc. Geol. Ass., Lond.*, **47** : 328–345, 1 fig.

DAVIS, A. G. & ELLIOTT, G. F. 1958. The palaeogeography of the London Clay sea. *Proc. Geol. Ass., Lond.*, **68** : 255–273, 2 figs.

DEFLANDRE, G. 1934. Sur les microfossiles d'origine planctonique conservés a l'état de matière organíque dans les silex de la craie. *C. R. Acad. Sci. Paris*, **199** : 966–968, 11 figs.

—— 1935. Considerations biologiques sur les micro-organismes d'origine planctonique conservés dans les silex de la craie. *Bull. Biol. Fr. Belg.*, Paris, **68** : 213—244, pls. 5–9.

—— 1936*a*. *Les flagellés fossiles. Aperçu biologique et paléontologique. Rôle géologique.* Actual. scient. et ind., Paris, no. 335. 98 pp., 135 figs.

—— 1936*b*. Microfossiles des silex crétacés. I. Generalités Flagellés. *Ann. Paléont.*, Paris, **25** : 151–191, pls. 11–20.

—— 1937. Microfossiles des silex crétacés. II. Flagellés incertae sedis. Hystrichosphaeridées. Sarcodines. Organismes divers. *Ann. Paléont.*, Paris, **26** : 51–103, pls. 8–18.

—— 1938. Microplancton des mers jurassiques conservé dans les marnes de Villers-sur-Mer (Calvados). *Trav. Stat. Zool. Wimereux*, Paris, **13** (*Vol. jubilaire M. Caullery*): 147–200, pls. 5–11.

—— 1939. Sur les dinoflagellés des schistes bitumineux d'Orbagnoux (Jura). *Bull. Soc. Fr. Microsc.*, Paris, **8** : 141–145, pl. 6.

—— 1946. Hystrichosphaeridés II. Espèces du Secondaire et du Tertiaire. *Fichier micropaléont.* (6) *Arch. orig. Serv. Docum. C.N.R.S.*, no. 235, cards 860–1019.

—— 1947. Sur quelques micro-organismes planctoniques des silex jurassiques. *Bull. Inst. Oceanogr. Monaco*, **921** : 1–10, figs. 1–5.

—— 1952. Protistes, Généralités. Sous-embranchement des Flagellés. Group Incertae Sedis. *In* Piveteau, J. (Ed.). *Traité de Paléontologie*, **1** : 89–95, 99–130, text-figs. 322–329.

—— 1964. Quelques observations sur la systématique et la nomenclature des dinoflagellés fossiles. *Multicop. E.P.H.E. et illustration C.N.R.S.* : 1–8.

DEFLANDRE, G. & COOKSON, I. C. 1955. Fossil microplankton from Australian late Mesozoic and Tertiary sediments. *Aust. J. Mar. Freshwater Res.*, Melbourne, **6** : 242–313, pls. 1–9.

DEFLANDRE, G. & COURTEVILLE, H. 1939. Note préliminaire sur les microfossiles des silex crétacés du Cambrésis. *Bull. Soc. Fr. Microsc.*, Paris, **8** : 95–106, pls. 2–4.

DEFLANDRE-RIGAUD, M. 1955. Microfossiles des silex sénoniens du Tréport (Seine-Maritime). *C.R. Somm. Soc. Géol. Fr.* Paris, **1–2** : 19–20.

DEUNFF, J. 1961. Un microplankton à Hystrichosphères dans le Tremadoc du Sahara. *Rev. Micropaléont.*, Paris, **4** : 37–52, pls. 1–3.

DOWNIE, C. 1957. Microplankton from the Kimeridge Clay. *Quart. J. Geol. Soc. Lond.*, **112** : 413–434, pl. 20.

DOWNIE, C., EVITT, W. R. & SARJEANT, W. A. S. 1963. Dinoflagellates, hystrichospheres and the classification of the Acritarchs. *Stanford Univ. Publ., Geol. Sciences*, Palo Alto, **7** : 1–16.

DOWNIE, C. & SARJEANT, W. A. S. 1963. On the interpretation and status of some Hystrichosphere genera. *Palaeontology*, London, **6** : 83–96.

——1964. Bibliography and index of fossil dinoflagellates and acritarchs. *Mem. Geol. Soc. Amer.*, Washington, **94** : 1–180.

DRUGG, W. S. 1964. *Glyphanodinium*, a new dinoflagellate genus from the Paleocene of California. *Proc. Biol. Soc. Washington*, **77** : 237–240, 6 figs.

EAGAR, S. H. & SARJEANT, W. A. S., 1963. Fossil hystrichospheres concentrated by sieving techniques. *Nature, Lond.*, **198** : 81.

EHRENBERG, C. G. 1838. Über das Massenverhaltnis der jetzt labenden Kieselinfusorien und uber ein neues Infusorien—Conglomerat als Polierschiefer von Jastraba in Ungarn. *Abh. Akad. Wiss. Berlin* (1836) **1** : 109–135, 2 pls.

—— 1843. Über einige Jura-Infusorien Arten des Korallrags bei Krakau. *Mber. Akad. Wiss. Berlin*, **1843** : 61–63.

—— 1854. *Mikrogeologie.* Leipzig. 486 pp., 41 pls.

EISENACK, A. 1935. Mikrofossilien aus Doggergeschieben Ostpreussens *Z. Geschiebeforsch.*, Berlin, **11** : 167–184, pls. 4, 5.

—— 1936. *Eodinia pachytheca* n.g. n. sp., ein primitiver Dinoflagellat aus einem Kelloway—Geschiebe Ostpreussens. *Z. Geschiebeforsch.*, Berlin, **12** : 72–75, 6 figs.

—— 1938. Die Phosphoritknollen der Bernsteinformation als überlieferer tertiären Planktons. *Schr. phys.-okon. Ges. Königsberg*, **70** : 181–188, figs. 1–6.

—— 1954. Mikrofossilien aus Phosphoriten des samlandischen Unter-Oligozäns und über die Einheitlichkeit der Hystrichosphären. *Palaeontographica*, Stuttgart (A) **105** : 49–95, pls. 7–12.

—— 1958. Mikroplankton aus dem norddeutschen Apt, nebst einigen Bemerkungen über fossile Dinoflagellaten. *N. Jb. Geol. Paläont. Abh.*, Stuttgart, **106** : 383–422, pls. 21–27.

—— 1959. Neotypen baltischer Silur-Hystrichosphären und neue Arten. *Palaeontographica*, Stuttgart (A) **112** : 193–211, pls. 15–17.

—— 1959*a*. Fossile Dinoflagellaten. *Arch. Crotistenk*, Jena, **104** : 43–50, pl. 3.

—— 1961. Einige Erorterungen uber fossile Dinoflagellaten nebst Ubersicht über die zur Zeit bekannten Gattungen. *N. Jb. Geol. Paläont., Abh.*, Stuttgart, **112** : 281–324, pls. 33–37.

—— 1963. Zur *Membranilarnax*—Frage. *N. Jb. Geol. Paläont., Mh.*, Stuttgart, **1963,** 2 : 98–103.

—— 1963*a*. Mitteilungen zur Biologie der Hystrichosphären und über neue Arten. *N. Jb. Geol. Paläont., Abh.*, Stuttgart, **118** : 207–216, pls. 19, 20.

—— 1963*b*. *Cordosphaeridium* n.g., ex *Hystrichosphaeridium*, Hystrichosphaeridea. *N. Jb. Geol. Paläont, Abh.*, Stuttgart, **118** : 260–265, pl. 29.

—— 1964. Erörterungen über einige Gattungen fossiler Dinoflagellaten und über die Einordnung der Gattungen in das System. *N. Jb. Geol. Paläont. Mh.*, Stuttgart, **1964,** 6 : 321–336, 3 figs.

Eisenack, A. & Cookson, I. C. 1960. Microplankton from Australian Lower Cretaceous sediments. *Proc. Roy. Soc. Victoria*, Melbourne, **72** : 1–11, pls. 1–3.

Eisenack, A. & Gocht, H. 1960. Neue Namen fur einige Hystrichosphären der Bernsteinformation Ostpreussens. *N. Jb. Geol. Paläont., Mh.*, Stuttgart, **1960,** 11 : 511–518, 4 figs.

Evitt, W. R. 1961. Observations on the morphology of fossil dinoflagellates. *Micropaleontology*, New York, **7** : 385–420, pls. 1–9.

—— 1963. A discussion and proposals concerning fossil dinoflagellates, hystrichospheres and acritarchs. *Proc. Nat. Acad. Sci.*, Washington, **49** : 158–164, 298–302, 4 figs.

Evitt, W. R. & Davidson, S. E. 1964. Dinoflagellate studies I. Dinoflagellate cysts and thecae. *Stanford Univ. Publ., Geol. Sci.*, Palo Alto, **10** : 1–12, pl. 1.

Firtion, F. 1952. Le Cenomanien inférieur de Nouvion-en-Thiérache; examen micropaléontologique. *Ann. Soc. Géol. Nord.*, Lille, **72** : 150–164, pls. 8–10.

Gerlach, E. 1961. Mikrofossilien aus dem Oligozän und Miozän Nordwestdeutschlands, unter besonderer Berücksichtigung der Hystrichosphaerideen und Dinoflagellaten. *N. Jb. Geol. Paläont., Abh.*, Stuttgart, **112** : 143–228, pls. 25–29.

Gocht, H. 1952. Hystrichosphaerideen und andere Kleinelebewesen aus Oligozän ablagerunger Nord-und Mitteldeutschlands. *Geologie*, Berlin, **1** : 301–320, pls. 1, 2.

—— 1955. *Rhombodinium* und *Dracodinium*, zwei nene Dinoflagellaten—Gattungen aus dem norddeutschen Tertiär. *N. Jb. Geol. Paläont., Mh.*, Stuttgart, 1955 : 84–92, 5 figs.

—— 1959. Miktroplankton aus dem nordwestdeutschen Neokom II. *Paläont. Z.*, Berlin, **33** : 50–89, pls. 3–8.

Gorka, H. 1963. Coccolithophoridés, dinoflagellés, hystrichosphaeridés, et microfossiles incertae sedis du Crétacé supérieur de Pologne. *Acta Palaeont. Polon.*, Warszawa, **8** : 3–90, pls. 1–11.

Hawkins, H. L. 1954. The Eocene succession in the eastern part of the Enborne valley, on the borders of Berkshire and Hampshire. *Quart. J. Geol. Soc. Lond.*, **110** : 409–430, pl. 19.

Kaye, P. 1963*a*. The ostracod genus *Neocythere* in the Speeton Clay. *Palaeontology*, London, **6** : 274–281, pl. 41.

—— 1963*b*. The ostracod species *Orthonotacythere inversa* (Cornuel) and its allies in the Speeton Clay of Yorkshire. *Palaeontology*, London, **6** : 430–439, pl. 61.

—— 1964*a*. Ostracods of the genera *Eucytherura* and *Cytheropteron* from the Speeton Clay. *Geol. Mag.*, London, **101** : 97–107, pls. 4, 5.

—— 1964*b*. Observations on the Speeton Clay (Lower Cretaceous). *Geol. Mag.*, London, **101** : 340–356, pls. 4, 5.

Klement, K. W. 1960. Dinoflagellaten und Hystrichosphaerideen aus dem Unteren und Mittleren Malm Südwestdeutschlands. *Palaeontographica*, Stuttgart (A) **114** : 1–104, pls. 1–10.

KLUMPP, B. 1953. Beitrag zur kenntnis der Mikrofossilien des Mittleren und Oberen Eozän. *Palaeontographica*, Stuttgart (A) **103** : 377–406, pls. 16–20.

LANTZ, J. 1958. Étude palynologique de quelques échantillons mésozoiques de Dorset (Grande-Bretagne). *Rev. Inst. Fr. Pétrôle*, Paris, **13** : 917–940, pls. 1–7.

LEJEUNE, M. 1937. L'étude microscopique des silex (2 ième Note). Un fossile anciennement connu et pourtant méconnu, *Hystrichosphaera ramosa* Ehrbg. *Ann. Soc. Géol. Belg.*, Liège, **60** : 239–260, pls. 1, 2.

LEJEUNE-CARPENTIER, M. 1938. L'étude microscopique des silex (6 ième Note). *Areoligera*; nouveau genre d'Hystrichosphaeridée *Ann. Soc. Géol. Belg.*, Liège, **62** : 163–174, 7 figs.

—— 1940. L'étude microscopique des silex (8 ième Note). Systématique et morphologie des " Tubifères ". *Ann. Soc. Géol. Belg.*, Liège, **63** : 216–236, 14 figs.

—— 1946. L'étude microscopique des silex (12 ième Note). Espèces nouvelles ou douteustes de *Gonyaulax*. *Ann. Soc. Géol. Belg.*, Liège, **69** : 187–197, 6 figs.

LOHMANN, H. 1904. Eier und sogenannte Cysten der Plankton-Expedition. Anhang : Cyphonautes. *Kiel : Wiss. Ergebnisse der Plankton-Expedition Humboldt-Stiftung* (N.S.) **4** : 1–62, pls. 1–7.

MACKÓ, S. 1963. Sporomorphs from Upper Cretaceous near Opole (Silesia) and from the London Clays. *Trav. Soc. Sci. Wroclaw* (B) **106** : 1–136, pls. 1–50.

MAIER, D. 1959. Planktonuntersuchungen in tertiären und quatären marinen Sedimenten. *N. Jb. Geol. Paläont., Abh.*, Stuttgart, **107** : 278–340, pls. 27–33.

MALIAVKINA, V. S., SAMOILOVITCH, S. R., *et al.*, 1961. Pollen and spores at Western Siberia ; Jurassic—Paleocene, A symposium (in Russian). *Trudy vses. Neft. Nauchno-Iss. Geol. Inst.*, **177** : 1–657, pls. 1–84 + I–XIV.

MANTELL, G. A. 1845. Notes on a microscopical examination of the Chalk and Flint of south-east England, with remarks on the Animalculites of certain Tertiary and modern deposits. *Ann. Mag. Nat. Hist.*, London, **16** : 73–88.

—— 1850. *A pictorial atlas of fossil remains, consisting of coloured illustrations selected from Parkinson's " Organic remains of a former World " and Artis's " Antediluvian Phytology "*. 208 pp., 74 pls. London.

—— 1854. *The Medals of Creation : or, first lessons in Geology and the study of organic remains.* 2nd edit. 2 vols. 930 pp., 6 pls. London.

MANUM, S. & COOKSON, I. C. 1964. Cretaceous microplankton in a sample from Graham Island, Arctic Canada, collected during the second " Fram "—Expedition (1898–1902), with notes on the microplankton from the Hassel Formation, Ellef Ringnes Island. *Skr. Norska. Vid.–Akad. Oslo, Mat.-Naturv. Kl.* (n.s.) **17** : 1–36, pls. 1–7.

MERRILL, J. A. 1895. Fossil sponges of the flint nodules in the Lower Cretaceous of Texas. *Bull. Mus. Comp. Zool. Harv.*, (*Geol. III*), Cambridge, Mass., **28** : 1–26, pl. 1.

NEALE, J. W. 1960. Marine Lower Cretaceous Ostracoda from Yorkshire, England. *Micropaleontology*, New York, **6** : 203–224, pls. 1–4.

—— 1960*a*. The Subdivision of the Upper D Beds of the Speeton Clay of Speeton, East Yorkshire. *Geol. Mag.*, London, **97** : 353–362.

—— 1962. Ostracods from the type Speeton Clay (Lower Cretaceous) of Yorkshire. *Micropaleontology*, New York, **8** : 425–484, pls. 1–13.

—— 1962*a* Ammonoidea from the Lower D Beds (Berriasian) of the Speeton Clay. *Palaeontology*, London, **5** : 272–296, pls. 40–45.

NEALE, J. W. & KILENYI, T. I. 1961. New Species of *Mandelstamia* (Ostracoda) from the English Mesozoic. *Palaeontology*, London, **3** : 439–449, pl. 71.

NEALE, J. W. & SARJEANT, W. A. S. 1962. Microplankton from the Speeton Clay of Yorkshire. *Geol. Mag.*, London, **99** : 439–458, pls. 19–20.

NORRIS, G. 1965. Archeopyle structures in Upper Jurassic dinoflagellates from southern England. *N.Z. J. Geol. Geophys.*, Wellington, **8** : 792–806.

NORRIS, G. & SARJEANT, W. A. S. 1965. *A descriptive index of genera of fossil Dinophyceae and Acritarcha.* Bull. N.Z. Geol. Surv. Palaeont., **40**. Wellington. 72 pp.

OYEN, F. H. VAN. 1964. *C.I.M.P. Groupe* 9. *Résumé de la réunion de travail, des* 25 *et* 26 *Novembre* 1964, *au Laboratoire Central de la C.F.P. à Bordeaux*. Secretariat of C.I.M.P. 62 pp. Pau.

PASTIELS, A. 1948. Contributions à l'étude des microfossiles de l'Eocene belge. *Mém. Mus. Roy. Hist. Nat. Belg.*, Bruxelles, **109** : 1–77. pls. 1–6.

PHILIPPOT, A. 1949. Contributions a la paléontologie des silex crétacés. Trois nouveaux microfossiles. *Bull. Soc. Sci. Bretagne*, Rennes, **24** : 55–58, 3 figs.

POCOCK, S. A. J. 1962. Microfloral analysis and age determination of strata at the Jurassic-Cretaceous boundary in the Western Canada plains. *Palaeontographica*, Stuttgart (B) **111** : 1–95, pls. 1–15.

PRESTWICH, J. 1847. On the probable age of the London Clay and its relations to the Hampshire and Paris Tertiary system. *Quart. J. Geol. Soc. Lond.*, **3** : 355–377, 2 figs.

PRITCHARD, A. 1841. *A history of Infusoria, living and fossil, arranged according to " Die Infusoriensthierchen " of C. G. Ehrenberg*. 439 pp., 12 pls. London.

READE, REV. J. B. 1839. On some new organic remains in the Flint of Chalk. *Ann. Nat. Hist.*, London, **2** : 191–198, pls. 8, 9.

REINSCH, P. F. 1905. Die Palinosphärien, ein mikroscopischer vegetabile Organismus in der Mukronatenkreide. *Cbl. Min. Geol. Paläont.* Stuttgart, **105** : 402–407, 2 figs.

REISSINGER, A. 1950. Die " Pollenanalyse " ausgedehnt auf alle Sediment-gesteine der geologischen Vergangenheit II. *Palaeontographica*, Stuttgart (B) **90** : 100–126, pls. 11–19.

ROSSIGNOL, M. 1962. Analyse pollonique de sédiments marins Quaternaires en Israël II. Sédiments Pleistocènes. *Pollen et Spores*, Paris, **4** : 121–148, pls. 1, 2.

—— 1964. Hystrichosphères du Quaternaire en Mediterranée orientale, dans les sédiments Pleistocènes et les boues marines actuelles. *Rev. Micropaléont.*, Paris, **7** : 83–99, pls. 1–3.

SARJEANT, W. A. S. 1959. Microplankton from the Cornbrash of Yorkshire. *Geol. Mag.*, London, **96** : 329–246, pl. 13.

—— 1960*a*. New hystrichospheres from the Upper Jurassic of Dorset. *Geol. Mag.*, London, **97** : 137–144, pl. 6.

—— 1960*b*. Microplankton from the Corallian rocks of Yorkshire. *Proc. Yorks. Geol. Soc.*, Leeds, **32** : 389–408, pls. 12–14.

—— 1961. Microplankton from the Kellaways Rocks and Oxford Clay of Yorkshire. *Palaeontology*, London, **4** : 90–118, pls. 13–15.

—— 1962*a*. Upper Jurassic microplankton from Dorset, England. *Micropaleontology*, New York, **8** : 255–268, pls. 1–2.

—— 1962*b*. Microplankton from the Ampthill Clay of Melton, South Yorkshire. *Palaeontology*, London, **5** : 487–497, pls. 69, 70.

—— 1963*a*. Fossil dinoflagellates from Upper Triassic sediments. *Nature, Lond.*, **199** : 353–354, 3 figs.

—— 1963*b*. Two new Jurassic species of *Gonyaulax* (Dinophyceae) *Rev. Micropaléont.*, Paris, **6** : 85–88, pl. 1.

—— 1964*a*. Proposal to conserve the generic names *Hystrichosphaera* Wetzel and *Hystrichosphaeridium* Defl. *Regnum Vegetabile*, Utrecht, 34 : 65–67.

—— 1964*b*. New name and diagnosis for an Upper Jurassic species of *Gonyaulacysta* (Dinophyceae). *Palaeontology*, London, **7** : 472–473.

—— 1965. The Xanthidia. *Endeavour*, London, **24** : 33–39, 19 figs.

SINGH, C. 1964. Microflora of the Lower Cretaceous Mannville Group, East-Central Alberta. *Bull. geol. Div. Res. Council Alberta*, Edmonton, **15** : 1–238, pls. 1–29.

STAPLIN, F. L. 1961. Reef-controlled distribution of Devonian microplankton in Alberta. *Palaeontology*, London, **4** : 392–424, pls. 48–51.

STAPLIN, F. L., JANSONIUS, J., & POCOCK, S. A. J. 1965. Evaluation of Some Acritarchous hystrichosphere genera. *N. Jb. Geol. Paläont. Abh.*, Stuttgart, **123** : 167–201, pls. 18–20.

TASCH, P. 1963. Hystrichosphaerids and dinoflagellates from the Permian of Kansas. *Micropaleontology*, New York, **9** : 332–336., pl. 1.

TASCH, P., MCCLURE, K. & OFTEDAHL, O. 1964. Biostratigraphy and taxonomy of a hystrichosphere–dinoflagellate assemblage from the Cretaceous of Kansas. *Micropaleontology*, New York, **10** : 189–206, pls. 1–3.

VALENSI, L. 1953. Microfossiles des silex du Jurassique moyen. Remarques pétrographiques. *Mém. Soc. Géol. Fr.*, Paris, **68** : 1–100, pls. 1–16.

—— 1955. Étude micropaléontologique des silex du Magdalénien de Saint-Amand (Cher). *Bull. Soc. Préhist. Fr.*, Paris, **52** : 584–596, pls. 1–5.

WALL, D. 1965. Microplankton, pollen and spores from the Lower Jurassic in Britain, *Micropaleontology*, New York, **11** : 151–190, pls. 1–9

WEILER, H. 1956. Über einem Fund von Dinoflagellaten, Coccolithophoriden und Hystrichosphaerideen im Tertiär des Rheintales. *N. Jb. Geol. Paläont., Abh.*, Stuttgart, **104** : 120–147, pls. 11–13.

WEST, R. G. 1961. Vegetational history of the Early Pleistocene of the Royal Society borehole at Ludham, Norfolk. *Proc. Roy. Soc.*, London (B) **155** : 437–453.

WETHERELL, E. W. 1892. On the occurrence of *Xanthidia* (*Spiniferites* of Mantell) in the London Clay of the Isle of Sheppey. *Geol. Mag.*, London (3) **9** : 28–30.

WETZEL, O. 1933. Die in organischer Substanz erhaltenen Mikro-fossilien des Baltischen Kreide-Feuersteins. *Palaeontographica*, Stuttgart, **77** : 141–188 ; 1–110, pls. 1–7.

—— 1935. Die Mikropaläontologie des Heiligenhafner Kieseltones (Unter-Eozän). *Jber. Niedersachs. Geol. Verein*, Hannover, **27** : 41–76, pls. 8–10.

—— 1948. Mikropaläontologische Funde in Gesteinsproben einer holsteinischer Bohrung, besonders in Kreide-und Keuperschichten. *N. Jb. Miner. Abh.*, Stuttgart, **89** : 315–343, pls. 33–38.

—— 1950. Deutungsversuche an ausgewahlten Grippen vorn Mikrofossilien und Mikrostrukturen im baltischen Geschiebe-Feuerstein und in einigen andere Gesteine der Kreidezeit. *N. Jb. Miner. Abh.*, Stuttgart, **91** : 161–192, pls. 11–13.

WETZEL, W. 1952. Beitrag zur Kenntnis des dan-zeitlichen Meeres-planktons. *Geol. Jahrb.*, Hannover, 66 : 391–419, pl. 1.

—— 1955. Die Dan-Scholle vom Katharinenhof (Fehmarn) und ihr Gehalt an Planktonen. *N. Jb. Geol. Paläont. Mh.*, Stuttgart, 1955, no. 1 : 30–46, 26 figs.

WHITE, H. H. 1842. On fossil Xanthidia. *Microsc. J.*, London, **11** : 35–40, pl. 4.

WHITE, H. J. O. 1921. A short account of the geology of the Isle of Wight. *Mem. Geol. Surv. G.B.*, London. 219 pp., 1 pl.

WILKINSON, S. J. 1849. Observations on *Xanthidium*, both fossil and recent. *Trans. Microsc. Soc. Lond.*, **2** : 89–92, pl. 3.

WIT, R. DE 1943. Hystrichosphaeridae in Limburgsche Vuursten. *Verh. Geol. Mijrib. Gen.*, Gravenhage, **13** : 363–392, 15 figs.

WRIGLEY, A. 1924. Faunal divisions of the London Clay. *Proc. Geol. Assoc. Lond.*, **35** : 245–259.

INDEX

New taxonomic names and the page numbers of the principal references are printed in **Bold** type. An asterisk (*) indicates a figure.

PLATE 1

FIG. 1. ***Hystrichosphaera ramosa*** (Ehrenberg) var. ***ramosa*** nov. Holotype. Slide xxv. Flint from Delitzsch. Humboldt-Universität, Berlin. ×400.

FIGS. 2, 3. ***Hystrichosphaera ramosa*** var. ***reticulata*** nov. Holotype. PF.3038(1). ×500. Fig. 3. Surface reticulation in focus. ×1250.

FIG. 4. ***Hystrichosphaera ramosa*** var. ***multibrevis*** nov. Cenomanian (boring depth, 670 feet). PF.3040(2). ×500.

FIG. 5. ***Hystrichosphaera ramosa*** var. ***gracilis*** nov. Cenomanian (boring depth, 670 feet). PF.3040(3). ×500.

FIG. 6. ***Hystrichosphaera ramosa*** var. ***ramosa*** nov. Cenomanian (boring depth, 730 feet). P.F.3033(3). ×500.

FIG. 7. ***Hystrichosphaera crassipellis*** Deflandre & Cookson. PF.3033(2). ×500.

FIG. 8. ***Hystrichosphaera crassipellis*** Deflandre & Cookson. Cenomanian (boring depth, 770 feet). Wall section to illustrate the unusual thickness. FM.770(1). ×975.

FIG. 9. ***Hystrichosphaera cingulata*** (O. Wetzel). PF.3039(1). ×500.

FIG. 10. ***Hystrichosphaera cingulata*** var. ***reticulata*** nov. PF.3039(2). ×500.

FIG. 11. ***Hystrichosphaera crassimurata*** sp. nov. Holotype, PF.3040(1). ×500.

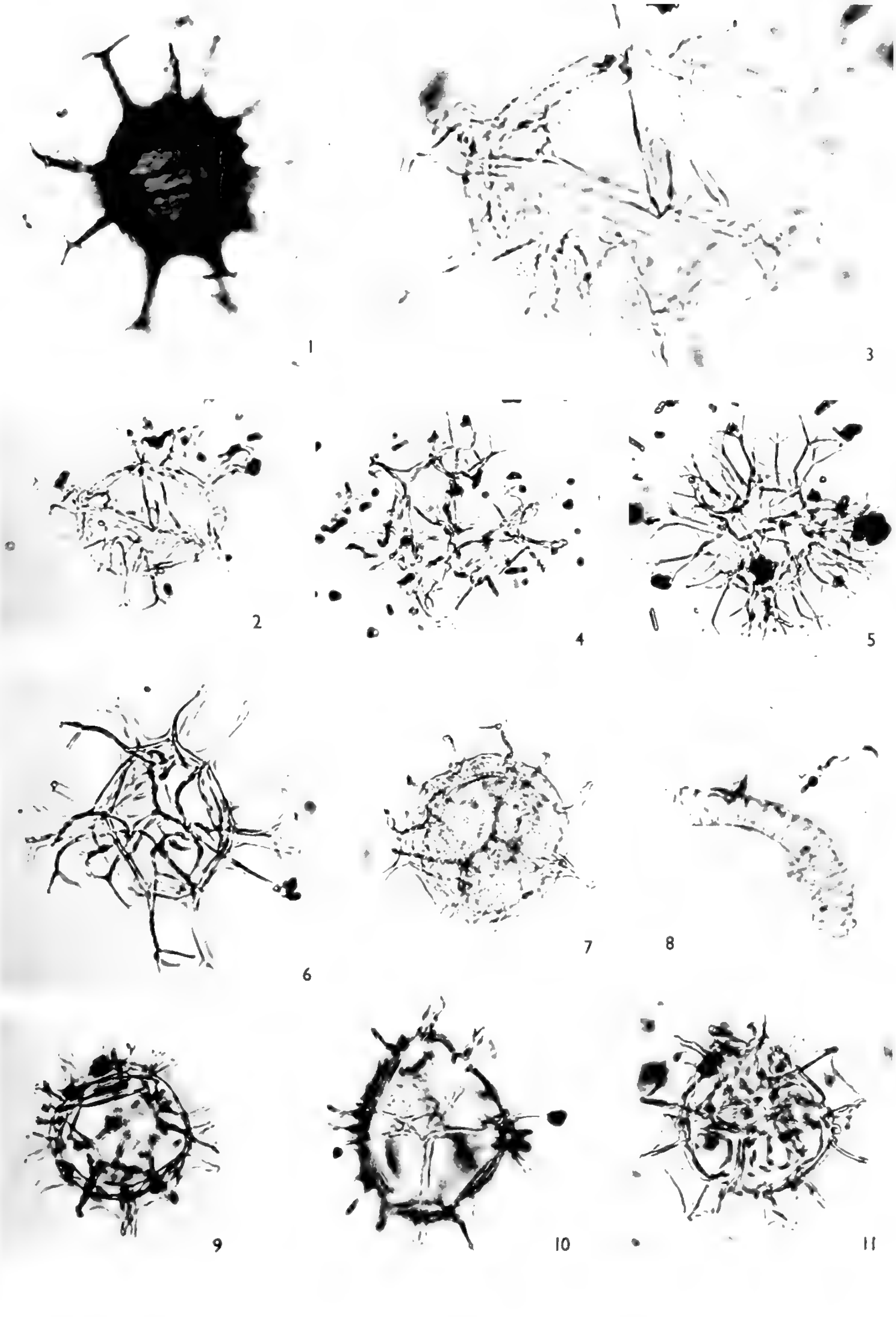


PLATE 2

FIGS. 1, 2. ***Achomosphaera sagena*** sp. nov. Holotype. PF.3041(1). Precingular archaeopyle shown. ×500. Fig. 2. Surface reticulation in focus. ×1250.

FIG. 3. ***Achomosphaera ramulifera*** (Deflandre). Cenomanian (boring depth, 840 feet). Precingular archaeopyle shown. FM.840(1). ×500.

FIG. 4. ***Hystrichosphaera cingulata*** var. ***reticulata*** nov. Cenomanian (boring depth, 730 feet). Lateral view, archaeopyle towards the north-west. PF.3039(2). ×5000.

FIG. 5. ***Cleistosphaeridium flexuosum*** sp. nov. Holotype, PF.3045(1). ×500 (phase contrast).

FIG. 6. ***Cleistosphaeridium heteracanthum*** (Deflandre & Cookson). PF.3041(2). Cenomanian (boring depth, 650 feet). Complete specimen showing form of processes. ×500 (phase contrast).

FIG. 7. ***Cleistosphaeridium heteracanthum*** (Deflandre & Cookson). Cenomanian (boring depth, 840 feet). FM.840/9. ×500.

FIGS. 8–10. ***Exochosphaeridium phragmites*** gen. et sp. nov. 8, Cenomanian (boring depth, 810 feet). Apical process and cingular processes present. PF.3043(1). ×500. 9, 10 Holotype, PF.3035(3). Precingular archaeopyle to the north-west and apical process to the south-west. ×500.

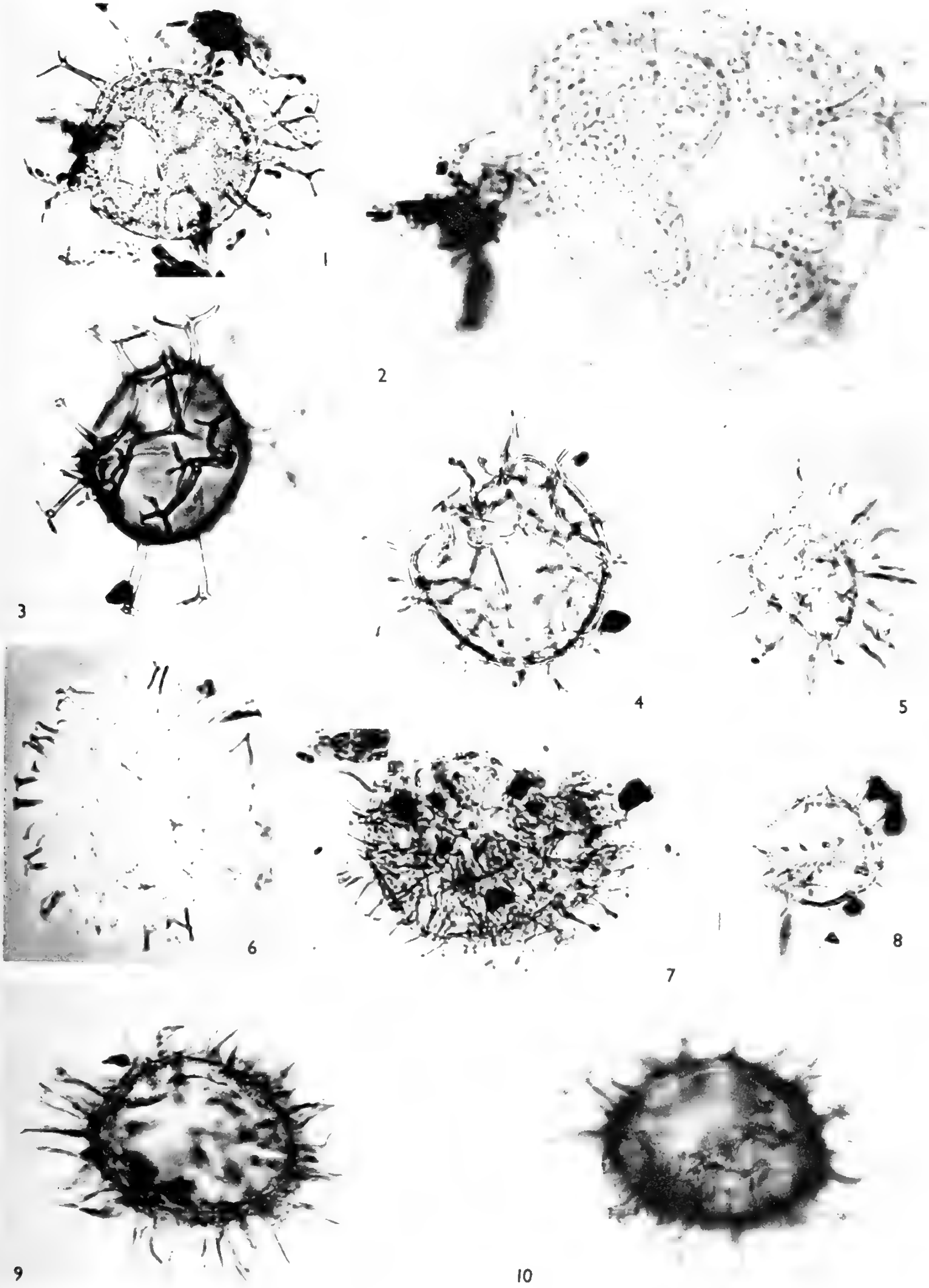

1
2
3
4
5
6
7
8
9
10

PLATE 3

FIG. 1. ***Hystrichosphaera ramosa*** var. ***ramosa*** nov. Upper Oxfordian, Throstler Clay. V.51714(1). ×500.

FIG. 2. ***Prolixosphaeridium deirense*** gen. et sp. nov. Holotype, V.51727(2). ×500.

FIG. 3. ***Tanyosphaeridium regulare*** sp. nov. Holotype, V.51755(1). ×500.

FIG. 4. ***Cordosphaeridiosum cracenospinosum*** sp. nov. Holotype, V.51748(1). ×200.

FIG. 5. ***Perisseiasphaeridium pannosum*** gen. et sp. nov. London Clay; Enborne boring (at 43·25 feet depth). E.11/71/9. ×525.

FIG. 6. ***Cordosphaeridium multispinosum*** sp. nov. Holotype, V.51751(1). ×500.

FIG. 7. ***Achomosphaera neptuni*** (Eisenack). V.51716(1). ×500.

FIG. 8. ***Cordosphaeridium gracilis*** (Eisenack). V.51746(1). ×312.

FIG. 9. ***Cordosphaeridium inodes*** (Klumpp). V.51745(1). Apical view. ×500.

PLATE 3

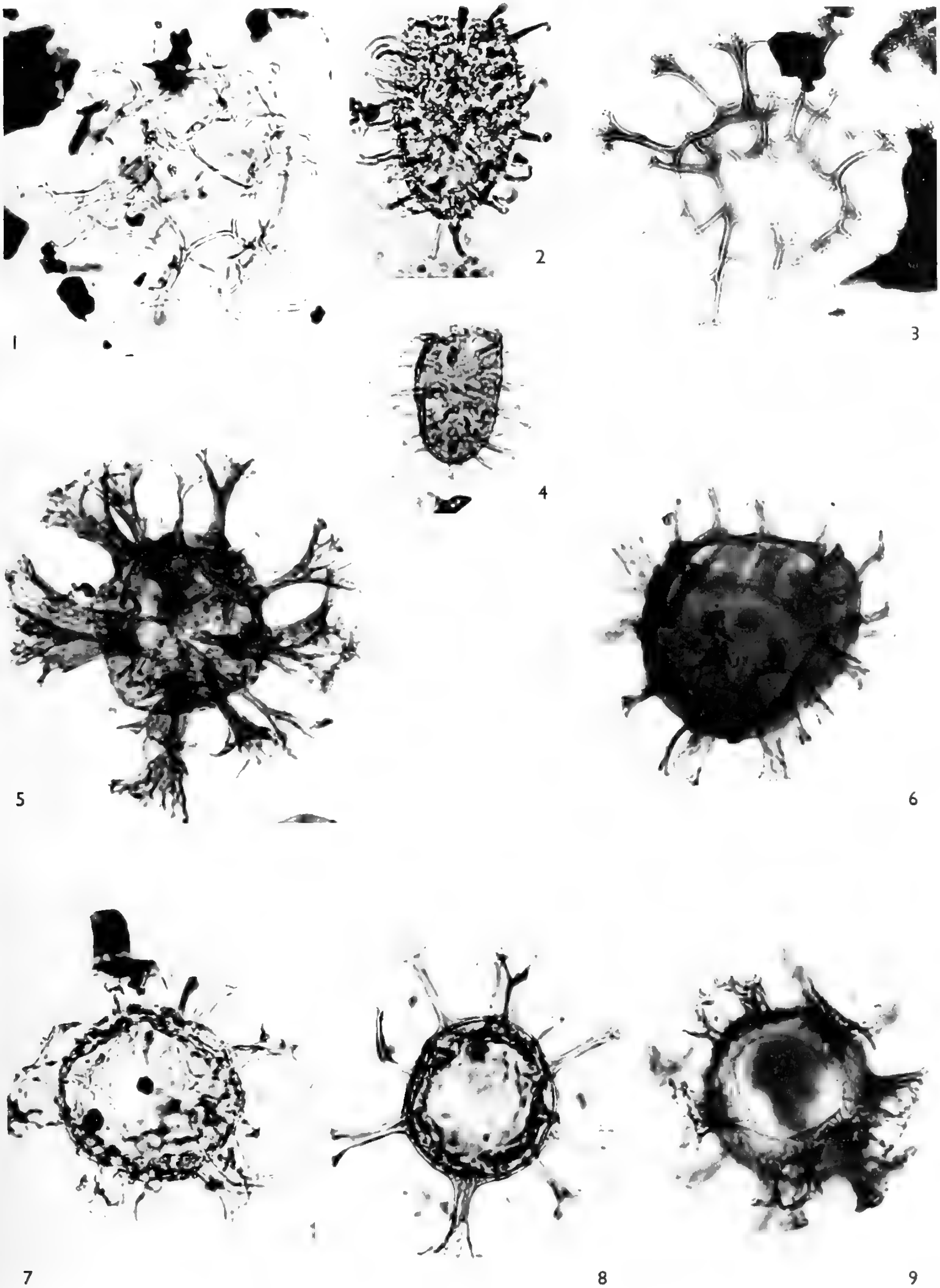


PLATE 4

FIG. 1. ***Hystrichosphaera buccina*** sp. nov. Holotype, V.51761(1). ×400.

FIG. 2. ***Diphyes colligerum*** (Deflandre & Cookson). V.51754(1). ×500.

FIG. 3. ***Diphyes colligerum*** (Deflandre & Cookson). London Clay; (85 feet above base of London Clay) Sheppey. Sh.3/1(1). Apical archaeopyle to the north-west. ×500.

FIG. 4. ***Hystrichosphaera ramosa*** var. ***granomembranacea*** nov. Holotype, V.51759(1). ×500.

FIG. 5. ***Hystrichosphaera cornuta*** var. ***laevimura*** nov. Holotype, V.51752(3). ×500.

FIG. 6. ***Hystrichosphaera ramosa*** var. ***multibreva*** nov. Holotype, V.51758(1). ×500.

FIG. 7. ***Hystrichosphaera cornuta*** Gerlach. V.51741(2). ×550.

FIG. 8. ***Hystrichosphaera ramosa*** var. ***membranacea*** (Rossignol). Membrane well developed on the apical pole. London Clay (173 feet above base of London Clay); Sheppey, Kent. Micropalaeont. Lab. Colln., University of Sheffield. ×375.

FIG. 9. ***Hystrichosphaera ramosa*** var. ***granosa*** nov. Holotype, V.51752(2). ×500.

FIG. 10. ***Polysphaeridium pastielsi*** sp. nov. Holotype, V.51753(1). ×425.

FIG. 11. ***Homotryblium tenuispinosum*** gen. et sp. nov. An isolated plate bearing a single intratabular process. London Clay; Enborne boring (at 53 feet depth). E.11/61/5(1). ×750.

FIG. 12. ***Hystrichosphaera ramosa*** var. ***membranacea*** (Rossignol). V.51747(2). ×500.

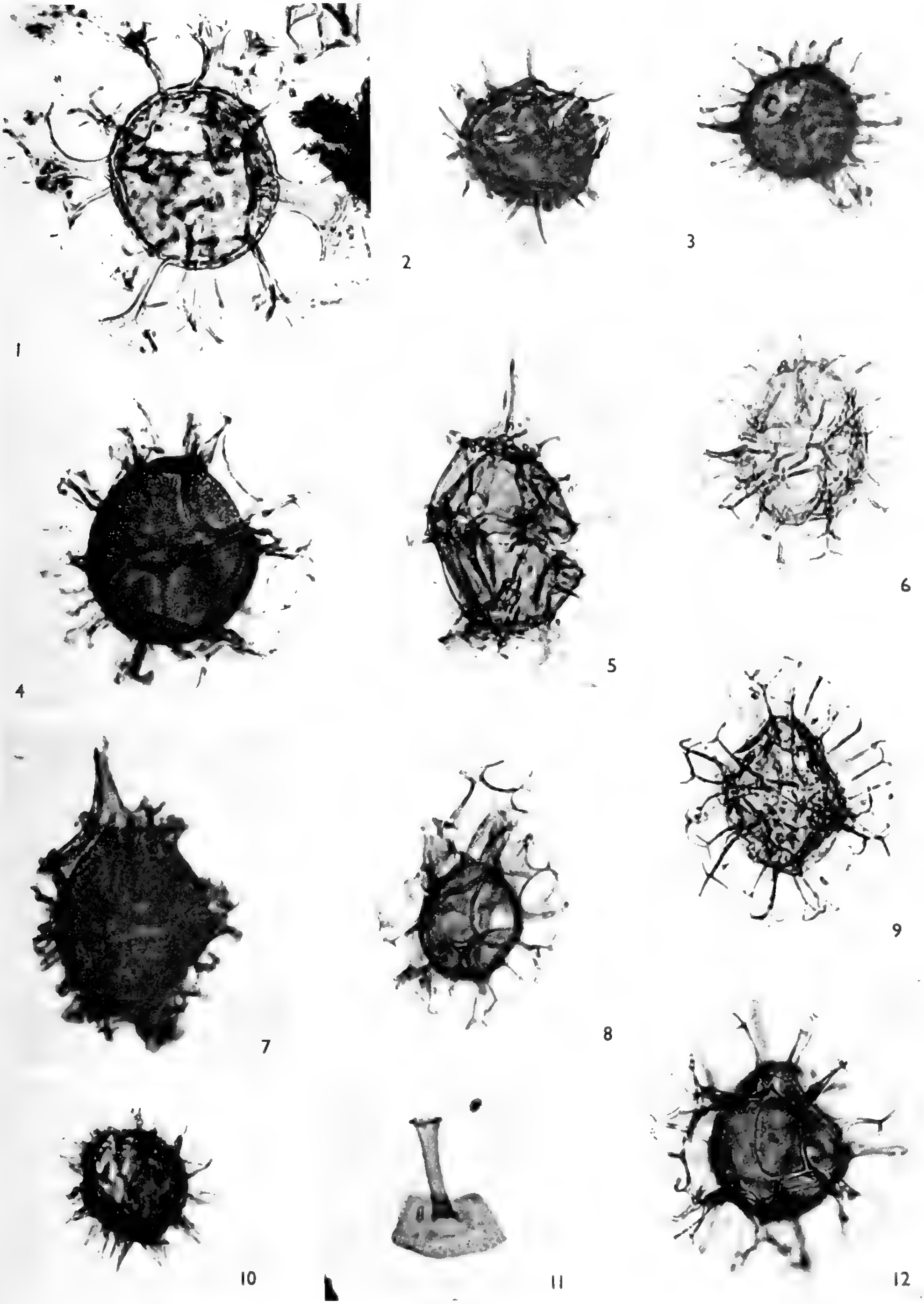


PLATE 5

FIG. 1. ***Achomosphaera ramulifera*** var. ***perforata*** nov. London Clay; Enborne (boring depth, 83·25 feet). Note precingular archaeopyle. WC.3/6(1). ×425.

FIG. 2. ***Hystrichosphaera monilis*** sp. nov. Holotype, V.51763(1), ×500.

FIG. 3. ***Achomosphaera alcicornu*** (Eisenack). V.51765(1). ×425.

FIG. 4. ***Achomosphaera ramulifera*** var. ***perforata*** nov. Holotype, V.51764(1). ×475.

FIG. 5. ***Cordosphaeridium fibrospinosum*** sp. nov. Holotype, V.51747(1). ×475.

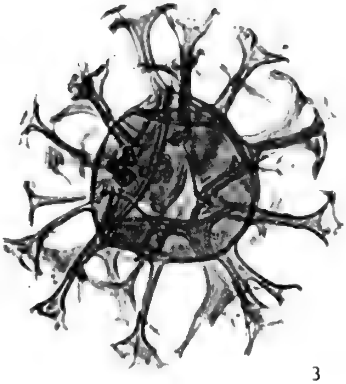
FIG. 6. ***Hystrichosphaera ramosa*** var. ***gracilis*** nov. Holotype, V.51757(1). ×350.

FIG. 7. ***Hystrichosphaera perforata*** sp. nov. Holotype, V.51760(1). ×550.

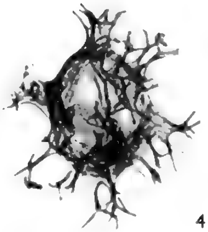
FIG. 8. ***Cordosphaeridium latispinosum*** sp. nov. Holotype, V.51746(2). ×640.

1

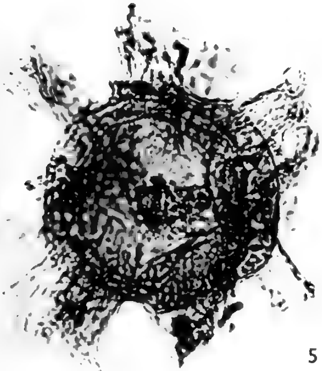
2



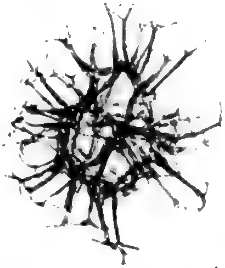
3



4

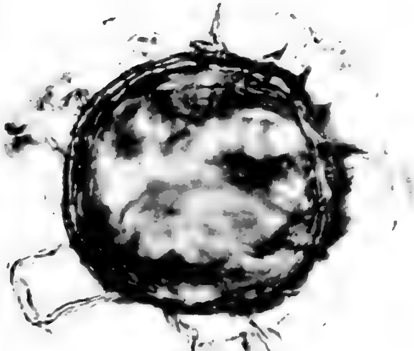


5



6

7



8

9

PLATE 6

FIG. 1. ***Hystrichosphaeridium tubiferum*** (Ehrenberg). Holotype. Slide XXV. Flint from Delitzsch. Humboldt-Universität, Berlin. Apical view. ×400.

FIG. 2. ***Hystrichosphaeridium tubiferum*** (Ehrenberg). Holotype. Medial view. ×400.

FIG. 3. ***Hystrichosphaeridium readei*** sp. nov. Holotype, PF.3030(2). ×500.

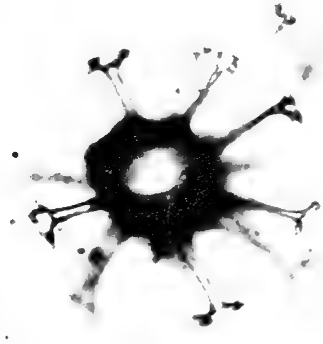
FIG. 4. ***Hystrichosphaeridium deanei*** sp. nov. Cenomanian (borehole depth, 690 feet). FM.690/12(2). ×400.

FIG. 5. ***Cleistosphaeridium ancoriferum.*** Cenomanian (borehole depth, 810 feet). PF.3044(1). ×500.

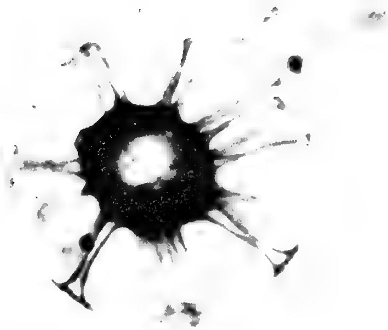
FIG. 6. ***Hystrichosphaeridium mantelli*** sp. nov. Holotype, PF.3032(1). ×500.

FIG. 7. ***Tanyosphaeridium variecalamum*** gen. et sp. nov. Holotype, PF.3035(2). ×500.

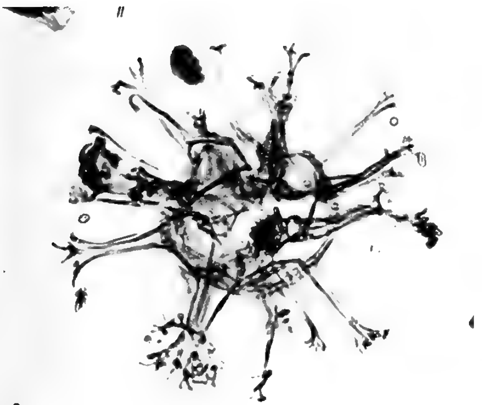
FIG. 8. ***Hystrichosphaeridium deanei*** sp. nov. Holotype, PF.3030(1). ×500.



1

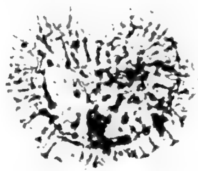


2

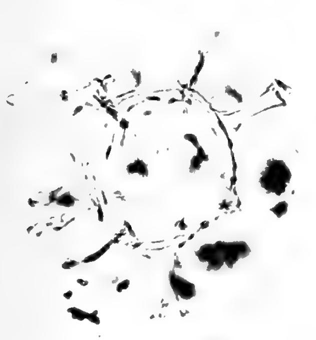


3

4



5



6

7

8

PLATE 7

FIG. 1. ***Oligosphaeridium complex*** (White). Neotype, lateral view. PF.3034(1) ×500.

FIG. 2. ***Oligosphaeridium complex*** (White). Cenomanian (borehole depth, 840 feet). Lateral view PF.3035(5). ×500.

FIG. 3. ***Polysphaeridium pumilum*** sp. nov. Holotype, PF.3037(1). ×975.

FIG. 4. ***Polysphaeridium pumilum*** sp. nov. Cenomanian (borehole depth, 770 feet). FM.770/7(1). ×975.

FIG. 5. ?***Cordosphaeridium fasciatum*** sp. nov. Holotype, V.51719(1). ×975.

FIG. 6. ?***Cordosphaeridium fasciatum*** sp. nov. Holotype. Nature of fibrous periphragm well shown. ×975.

FIG. 7. ***Litosphaeridium siphoniphorum*** (Cookson & Eisenack). Cenomanian (borehole depth 750 feet). Apical view showing 6-sided archaeopyle surrounded by 6 precingular processes. PF.3037(3). ×500.

FIG. 8. ***Litosphaeridium siphoniphorum*** (Cookson & Eisenack). Cenomanian (bore hole depth, 770 feet). Antapical view. FM.770/1(1). ×500.

FIG. 9. ***Hystrichosphaeridium radiculatum*** sp. nov. Cenomanian (borehole depth, 690 feet). PF.3030(3). ×500.

FIG. 10. ***Oligosphaeridium reticulatum*** sp. nov. Holotype, lateral view, PF.3035(1). ×500.

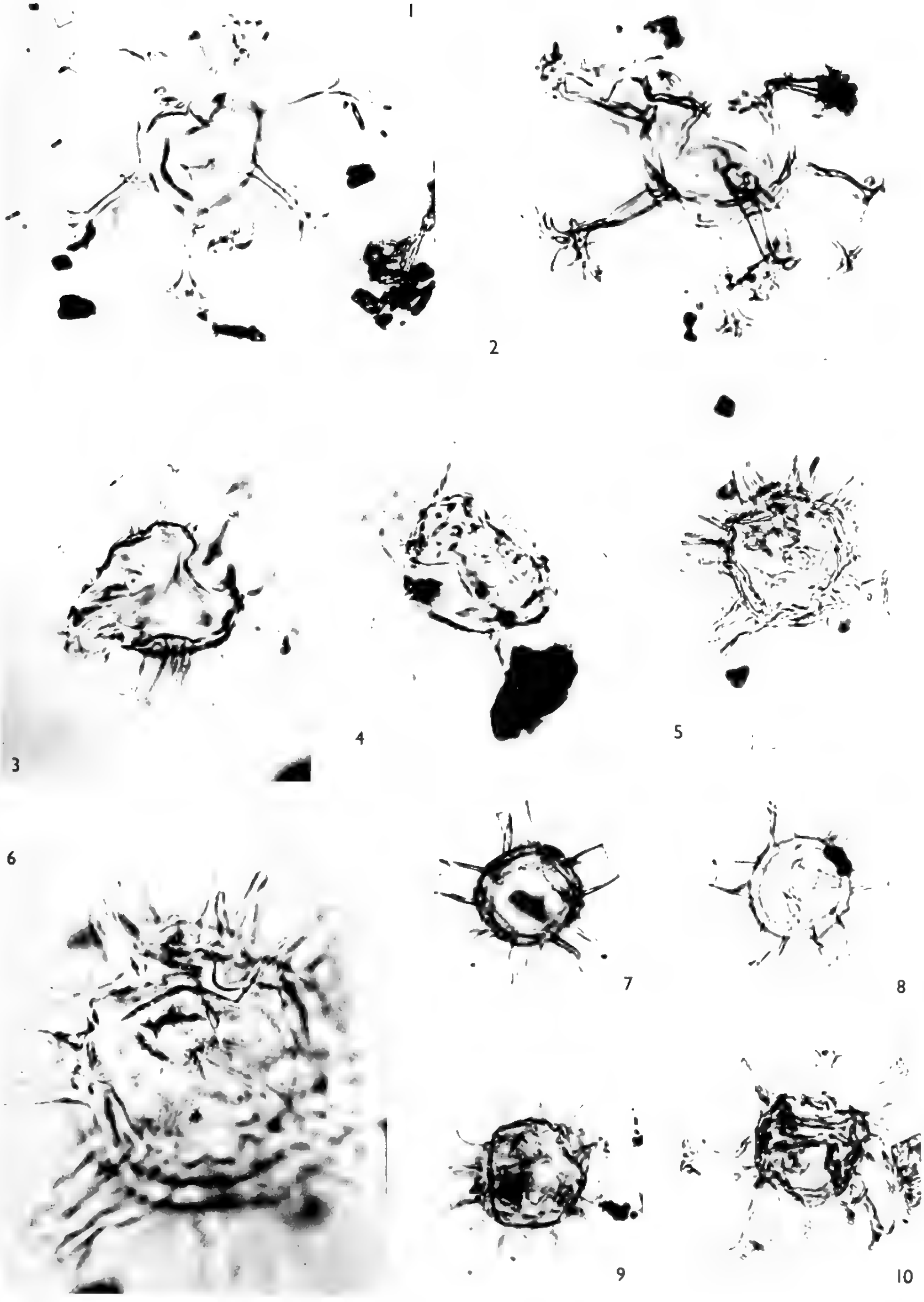


PLATE 8

FIG. 1. ***Hystrichosphaeridium bowerbanki*** sp. nov. Cenomanian (borehole depth, 750 feet). FM.750/2(1). ×500.

FIG. 2. ***Oligosphaeridium prolixispinosum*** sp. nov. Cemonanian (borehole depth, 750 feet). PF.3037(2). ×500.

FIG. 3. ***Oligosphaeridium prolixispinum*** sp. nov. Holotype, PF.3036(1). ×500.

FIG. 4. ***Hystrichosphaeridium bowerbanki*** sp. nov. Holotype, PF.3033(1). ×500.

FIG. 5. ***Hystrichosphaeridium tubiferum*** (Ehrenberg). Cenomanian (borehole depth, 690 feet). FM.690/12(1). ×500.

FIG. 6. ***Hystrichosphaeridum radiculatum*** sp. nov. Holotype, PF.3031(1). ×500.

FIG. 7. ***Surculosphaeridium longifurcatum*** (Firtion). Cenomanian (borehole depth, 730 feet). Antapical view. FM.730/2(1). ×500.

FIG. 8. ***Polysphaeridium laminaspinosum*** sp. nov. Holotype, PF.3052(1). ×975. (Phase contrast).

FIG. 9. ***Callaiosphaeridium asymmetricum*** (Deflandre & Courteville). Cenomanian (boring depth, 840 feet). Medial view in focus to show 6 large tubular cingular processes. FM.840/6(1). ×500.

FIG. 10. Antapical view of same showing 5 postcingular processes. ×500.

FIG. 11. ***Surculosphaeridium longifurcatum*** (Firtion) PF.3042(1) Cenomanian (boring depth, 840 feet). Lateral view showing 3 series of processes—precingular, cingular and post-cingular. ×500.

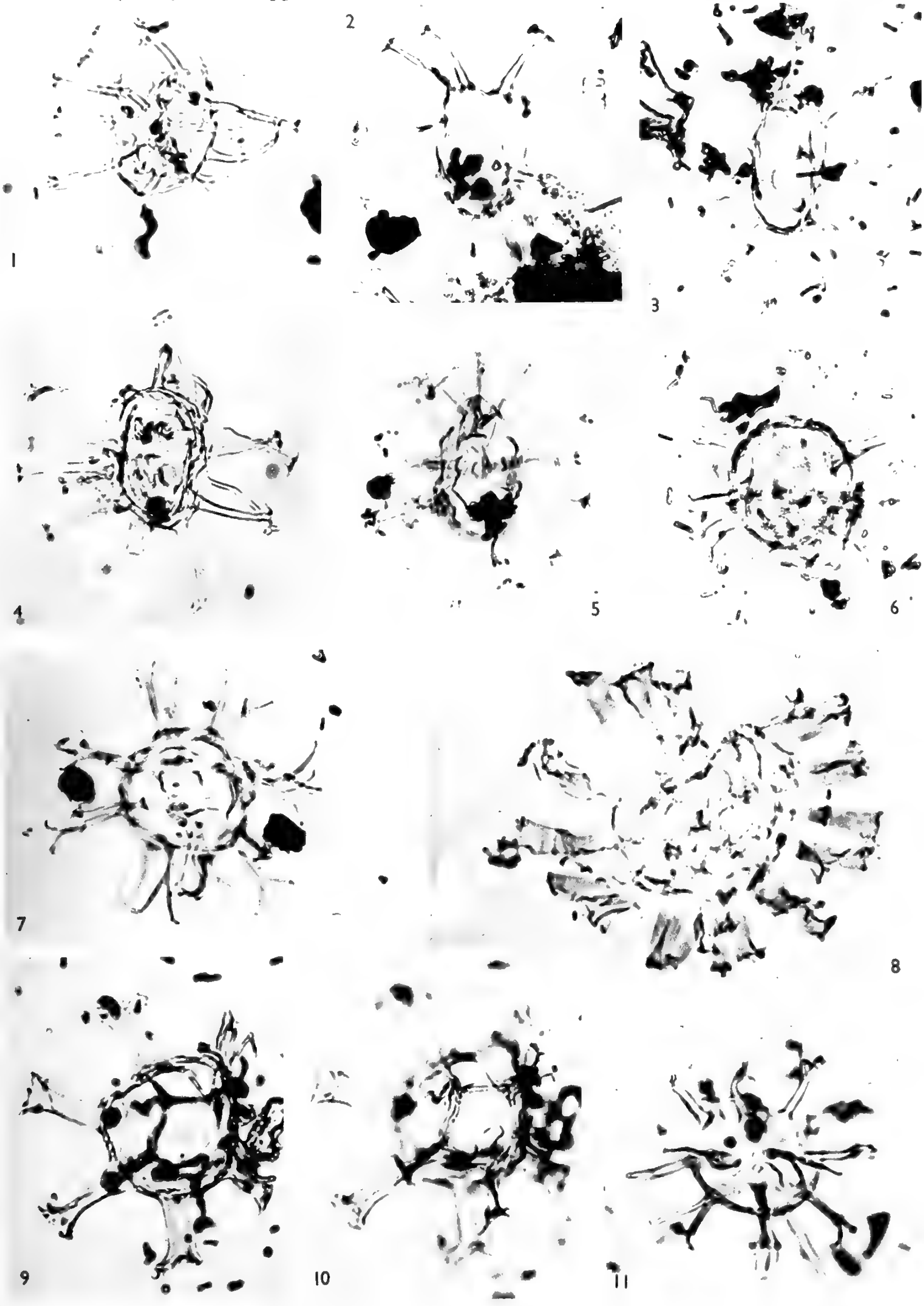

1
2
3
4
5
6
7
8
9
10
11

PLATE 9

FIG. 1. ***Cleistosphaeridium ancoriferum*** (Cookson & Eisenack). Cenomanian (boring depth, 690 feet). Detached 6-sided apical region. FM.690/4(1). ×1250. (Phase contrast).

FIG. 2. ***Callaiosphaeridium asymmetricum*** (Deflandre & Courteville). Speeton Clay (at 10·325 metres depth). V.51716(2). ×500.

FIG. 3. ***Hystrichosphaeridium simplicispinum*** sp. nov. V.51729(2). ×500.

FIG. 4. ***Oligosphaeridium macrotubulum*** (Neale & Sarjeant). Holotype, V.51712(2). ×400.

FIG. 5. ***Hystrichosphaeridium arborispinum*** sp. nov. Speeton Clay (at 42·5 feet depth). V.51719(3). ×500.

FIG. 6. ***Surculosphaeridium cribrotubiferum*** (Sarjeant). Holotype, V.51735(1). ×500.

FIG. 7. ***Oligosphaeridium vasiformum*** (Neale & Sarjeant). Holotype, V.51709(1). ×400.

FIG. 8. ***Surculosphaeridium vestitum*** (Deflandre). V.51736(1). ×500.

FIG. 9. ***Hystrichosphaera*** sp. V.51724(1). ×500.

FIG. 10. ***Hystrichosphaeridium arborispinum*** sp. nov. Holotype, V.51727(3). Lateral view. ×500.

FIG. 11. ***Achomosphaera neptuni*** (Eisenack). V.51717(1). Precingular archaeopyle to the north. ×500.

PLATE 9

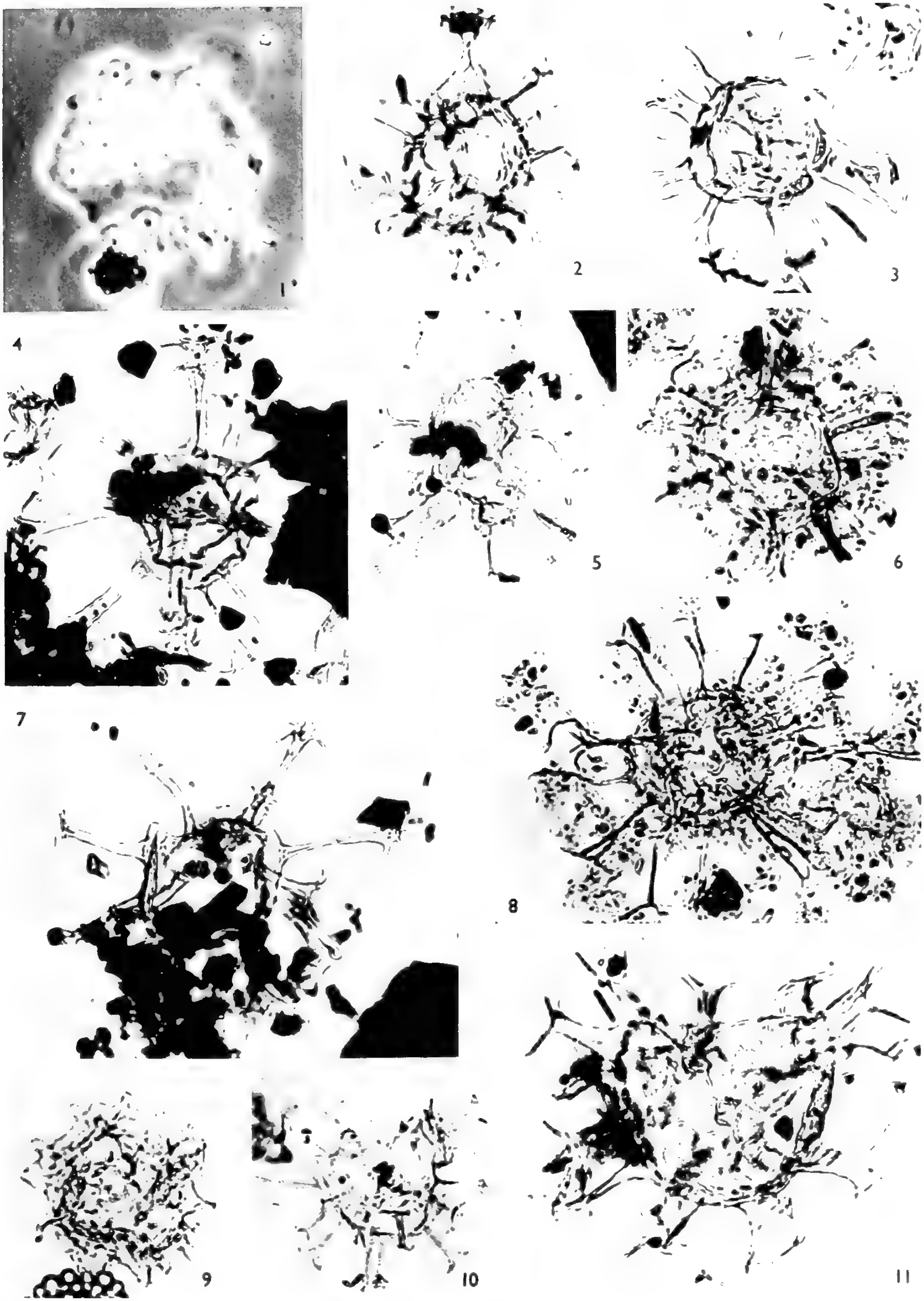


PLATE 10

FIG. 1. ***Oligosphaeridium vasiformum*** (Neale & Sarjeant). Holotype, V.51709(3). Two precingular processes missing. ×400.

FIG. 2. ***Hystrichosphaeridium tubiferum*** (Ehrenberg). London Clay ; (5 feet above base of London Clay) Sheppey. Sh.1/2(1). ×425.

FIG. 3. ***Oligosphaeridium complex*** (White). London Clay ; (146 feet above base of London Clay) Whitecliff Bay. Apical archaeopyle (sutural notch to the west) surrounded by 6 precingular processes. WC.16/1(1). ×425.

FIG. 4. ***Hystrichosphaeridium costatum*** sp. nov. Holotype, V.51708. ×500.

FIG. 5. ***Hystrichosphaeridium patulum*** sp. nov. Holotype, V.51739(1). ×1250.

FIG. 6. ***Hystrichosphaeridium salpingophorum*** (Deflandre). V.51734(1). ×500.

FIG. 7. ***Cleistosphaeridium diversispinosum*** gen. et sp. nov. Holotype, V.51750(1). ×400.

FIG. 8. ***Hystrichosphaeridium latirictum*** sp. nov. Holotype, V.51740(1). ×975.

FIG. 9. ***Oligosphaeridium pulcherrimum*** (Deflandre & Cookson). London Clay (78 feet above base of London Clay); Sheppey. Positions of the processes well shown, the absence of cingular processes being noticeable. Sh.2/5(1). ×875.

FIG. 10. ***Hystrichosphaeridium tubiferum*** var. ***brevispina*** nov. Holotype, V.51738(1). ×500.

PLATE 10

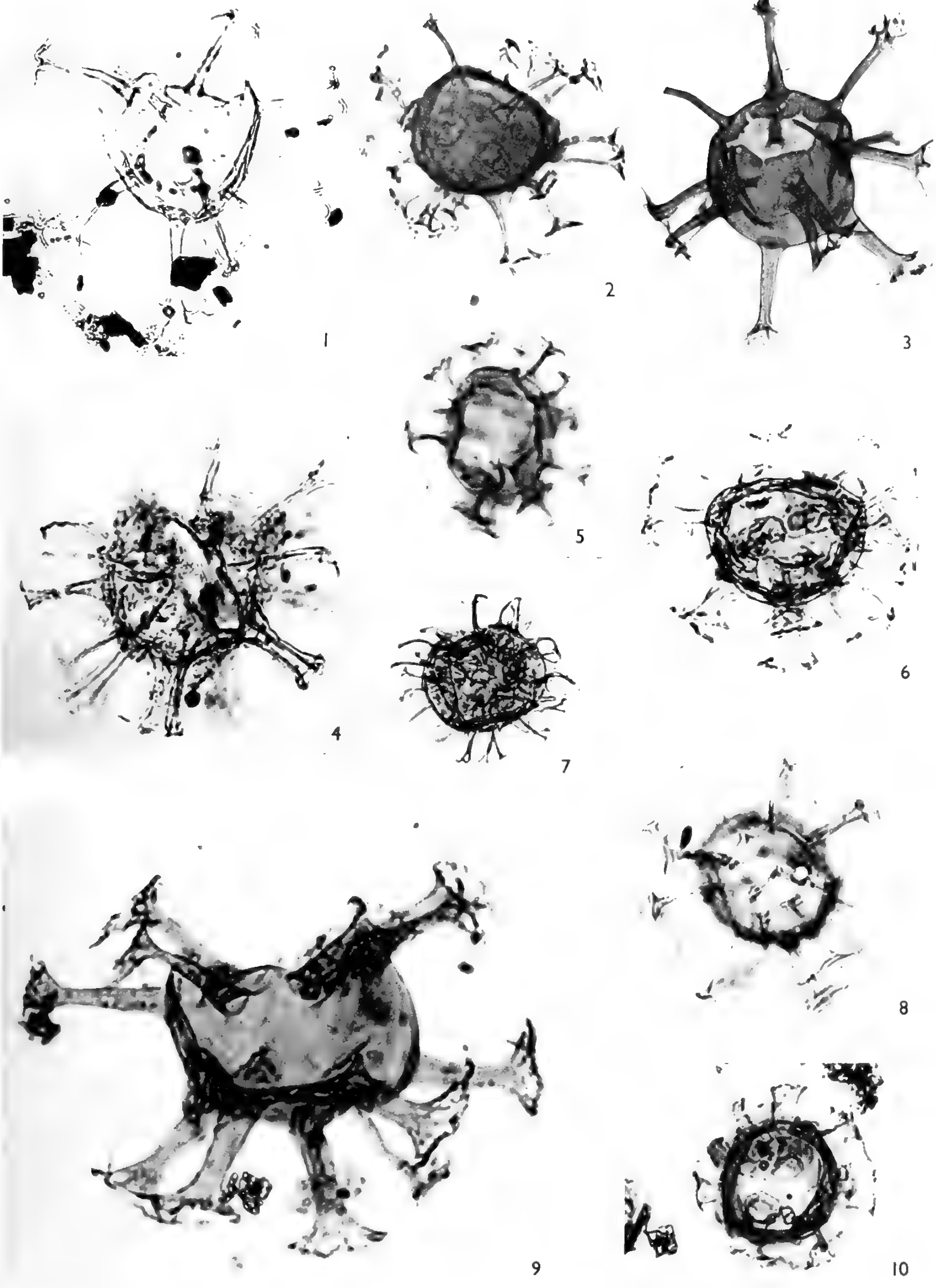


PLATE 11

FIG. 1. ***Polysphaeridium subtile*** gen. et sp. nov. Holotype, V.51752(1). ×850.

FIG. 2. ***Cordosphaeridium exilimurum*** sp. nov. London Clay (275 feet above base of London Clay) ; Whitecliff Bay. Archaeopyle well shown. V.51749(1). ×425.

FIG. 3. ***Hystrichosphaeridium sheppeyense*** sp. nov. Holotype, V.51741(1). ×850.

FIG. 4. ***Cordosphaeridium gracilis*** (Eisenack). London Clay (731 feet above base of London Clay); Sheppey. Detached apical plate. Sh.5/1(1). ×450.

FIG. 5. ***Oligosphaeridium pulcherrimum*** (Deflandre & Cookson). V.51742(1). Operculum only slightly displaced and bearing 4 apical processes.

FIG. 6. ***Cordosphaeridium gracilis*** (Eisenack). London Clay (173 feet above base of London Clay); Sheppey. Haplotabular archaeopyle well shown. V.51746(3). ×400.

FIG. 7. ***Cordosphaeridium gracilis*** (Eisenack). London Clay (173 feet above base of London Clay); Sheppey. Detached apical plate showing characteristic shape. Sh.5/1(2). ×450.

FIG. 8. ***Perisseiasphaeridium pannosum*** gen. et sp. nov. Holotype, V.51743(1). ×500.

FIG. 9. ***Cleistosphaeridium disjunction*** sp. nov. Holotype, V.51739(2). ×400.

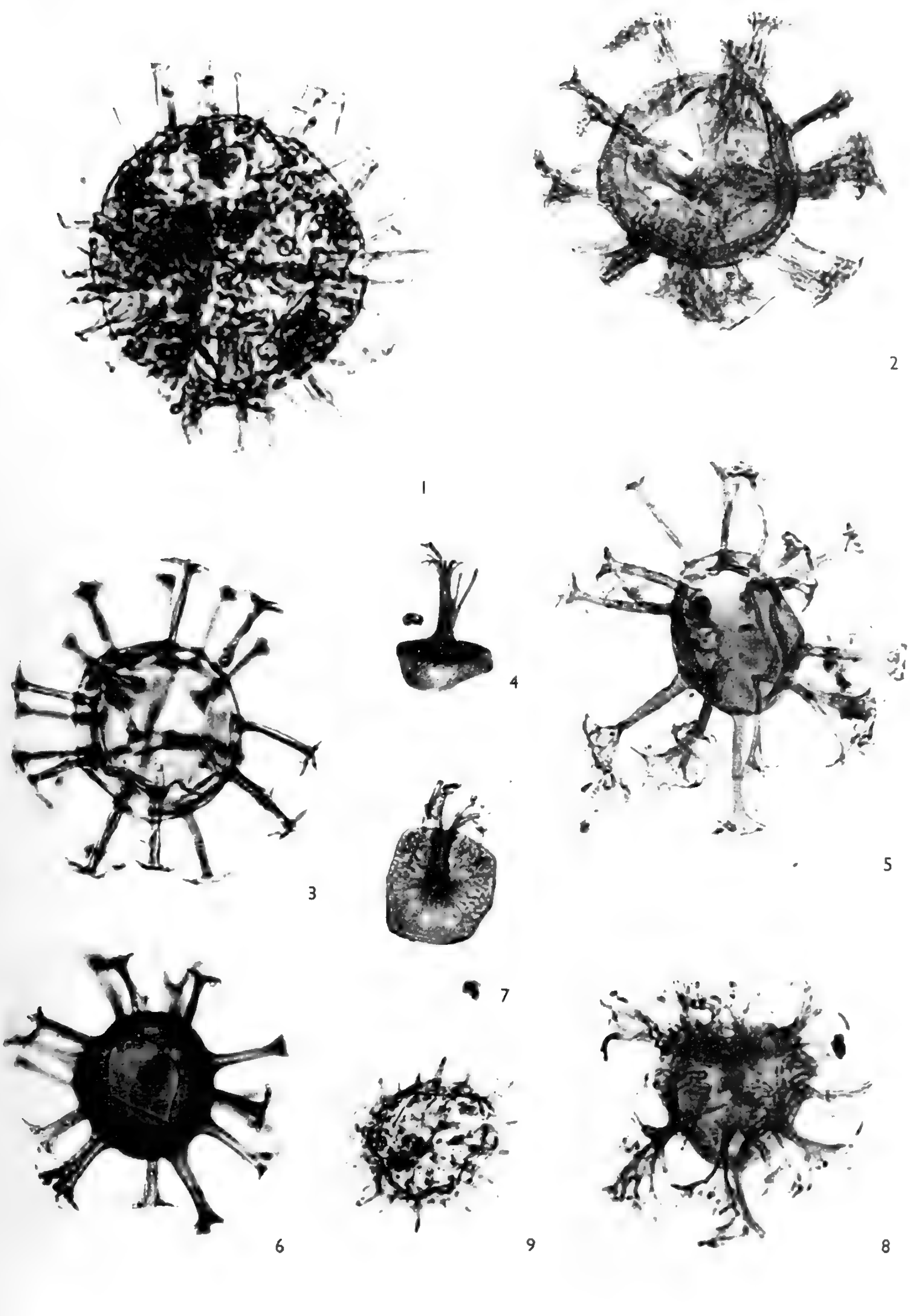

2
1
4
3
5
7
6
9
8

PLATE 12

FIG. 1. ***Homotryblium tenuispinosum*** sp. nov. London Clay ; Enborne (boring depth, 53 feet). Complete specimen showing medial rupture. V.51756(3). ×500.

FIG. 2. ***Cordosphaeridium divergens*** (Eisenack). London Clay ; Whitecliff, Isle of Wight. V.51750(1). ×500.

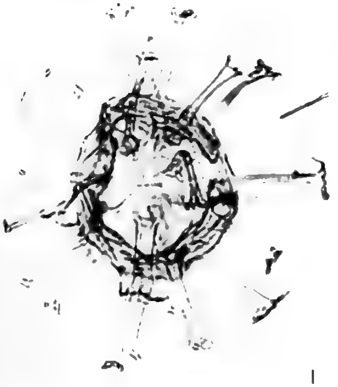
FIG. 3. ?***Litosphaeridium inversibuccinum*** sp. nov. Holotype, V.51744(1). Archaeopyle shown. ×975.

FIG. 4. ***Homotryblium pallidum*** sp. nov. London Clay ; Enborne (boring depth, 53 feet). Epitractal operculum bearing apical and precingular processes. V.51759(5). ×700.

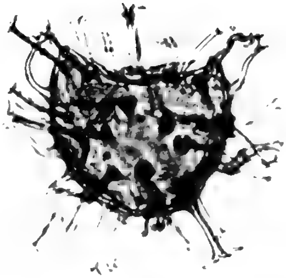
FIG. 5. ***Homotryblium tenuispinosum*** sp. nov. Holotype, V.51756(1). ×700.

FIG. 6. ***Homotryblium pallidum*** sp. nov. Holotype, V.51756(1). ×800.

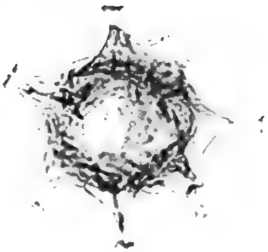
FIG. 7. ***Homotryblium tenuispinosum*** sp. nov. London Clay (78 feet above base of London Clay) ; Sheppey. Enlargement of part of the epitract to show that it is composed of a number of polygonal plates, each bearing a single intratabular process. V.51759(4). ×1200.



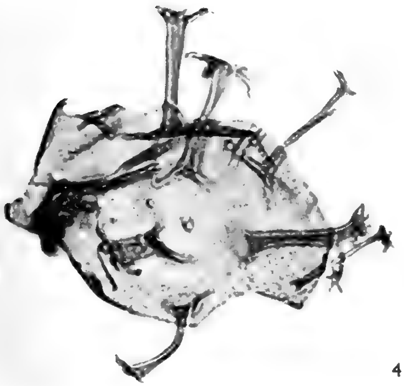
1



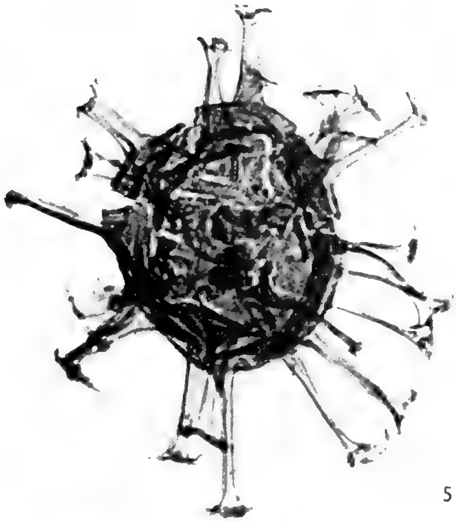
2



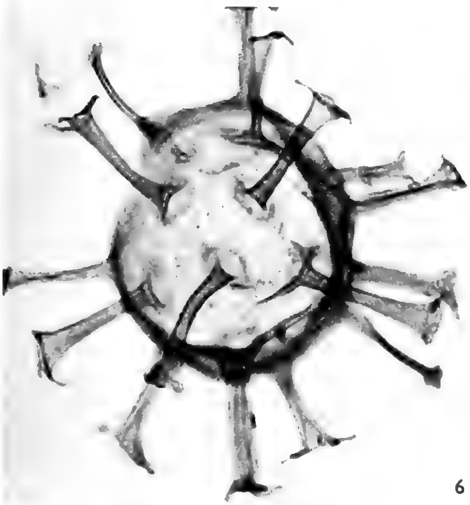
3



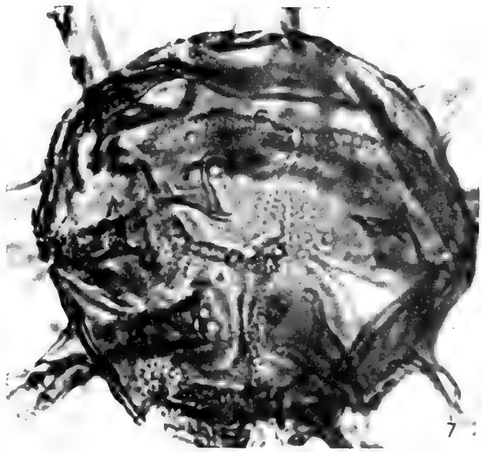
4



5



6



7

PLATE 13

Gonyaulacysta gongylos sp. nov.

FIG. 1. Ventral surface of holotype, V.51708(1). ×500.

FIG. 2. Dorsal surface of holotype viewed by transparency. ×500.

Gonyaulacysta palla sp. nov.

FIG. 3. Ventral surface of holotype, V.51718(2). ×500.

FIG. 4. Dorsal surface of holotype. ×500.

Gonyaulacysta aichmetes sp. nov.

FIG. 5. Ventral surface of holotype, V.51730(2). ×500.

FIG. 6. Dorsal surface of holotype. ×500.

Gonyaulacysta helicoidea (Eisenack & Cookson)

FIG. 7. Ventral surface of specimen, V.51718(1). ×500.

FIG. 8. Dorsal surface of same, viewed by transparency. ×500.

Gonyaulacysta episoma sp. nov.

FIG. 9. Ventral surface of holotype, V.51730(1).

FIG. 10. Dorsal surface of holotype, viewed by transparency. ×500.

Gonyaulacysta axicerastes sp. nov.

FIG. 11. Ventral surface of holotype, V.51727(1). ×500.

FIG. 12. Dorsal surface of holotype, viewed by transparency. ×500.

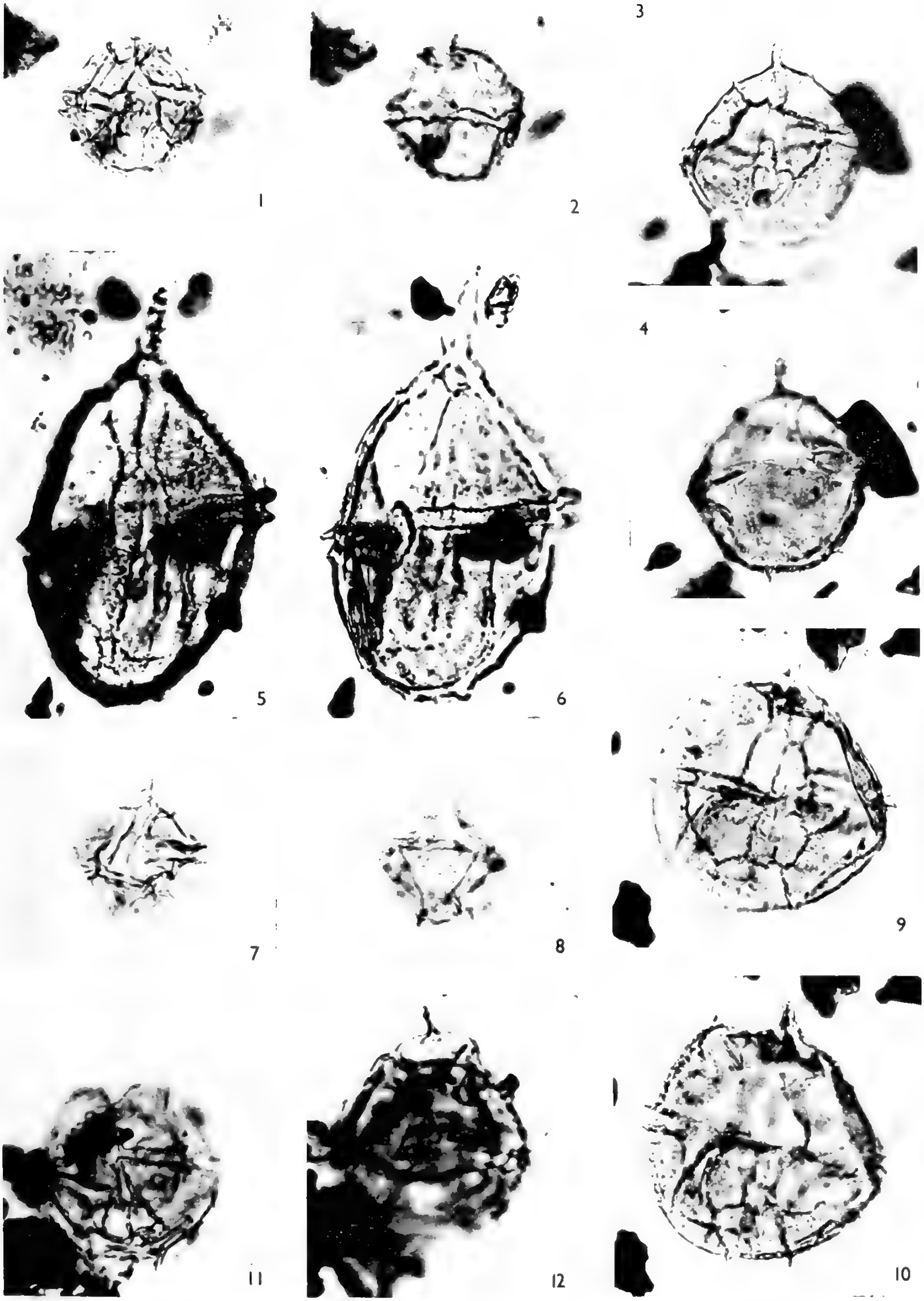

1
2
3
4
5
6
7
8
9
10
11
12

PLATE 14

Gonyaulacysta hadra sp. nov.

FIG. 1. Dorsal surface of the holotype, V.51731(1). The archaeopyle cover is within the shell. ×500.

Gonaulacysta whitei sp. nov.

FIG. 2. Ventral surface of the holotype, PF.3048(1).

Gonyaulacysta cassidata (Eisenack & Cookson)

FIG. 3. Ventral surface of specimen PF.3047(1), viewed by transparency. ×500.

FIG. 4. Dorsal surface of same. ×500.

Gonyaulacysta orthoceras (Eisenack)

FIG. 5. Ventral surface of specimen, V.51730(3). ×500.

FIG. 6. Dorsal surface of same, viewed by transparency. ×500.

Psaligonyaulax deflandrei gen. et. sp nov.

FIG. 7. Ventral surface of the holotype, PF.3049(1). ×500.

FIG. 8. Dorsal surface of same, viewed by transparency. ×500.

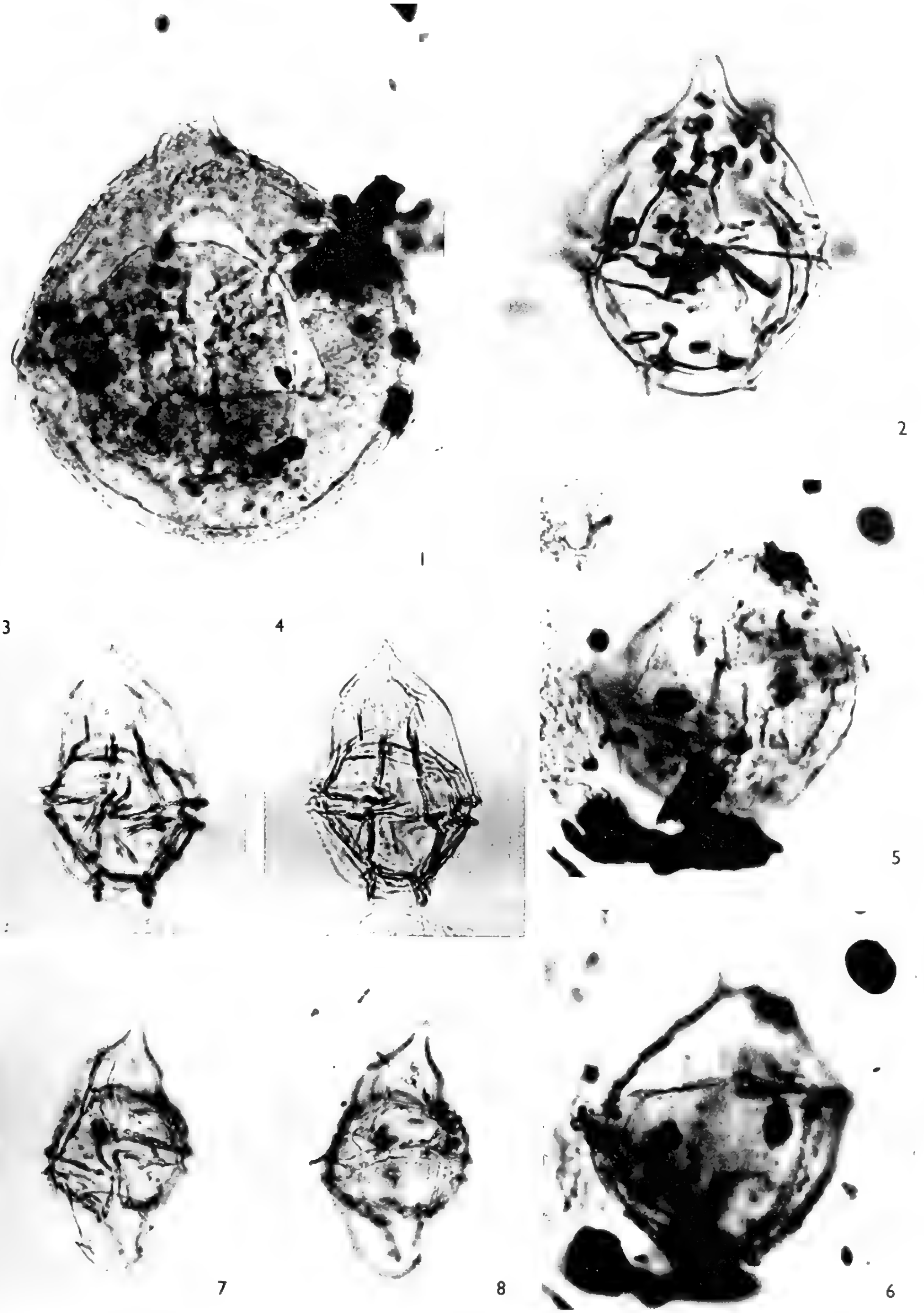

1
2
3
4
5
6
7
8

PLATE 15

Gonaylacysta fetchamense sp. nov.

FIG. 1. Ventral surface of holotype, PF.3046(1). ×500.

FIG. 2. Dorsal surface of same, viewed by transparency. ×500.

Leptodinium alectrolophum sp. nov.

FIG. 3. Ventral surface of paratype, V.51725(1). ×500.

FIG. 4. Dorsal surface of same, viewed by transparency. ×500.

FIG. 5. Oblique view of dorsal surface of holotype, V.51735(1). ×500.

FIG. 6. Oblique view by transparency of the ventral surface of same. ×500.

Meiourogonyaulax valensii gen. et sp. nov.

FIG. 7. Ventral surface of holotype. B.S.60 (Laboratoire de Micropaléontologie, École Pratique des Hautes Études, Paris). Photo. by Prof. G. Deflandre, reproduced by his permission. ×c.700.

Gonyaulacysta helicoidea (Eisenack & Cookson)

FIG. 8. Specimen, V.51728(1), in oblique ventral view. ×500.

FIG. 9. The same specimen, in oblique dorsal view, by transparency. ×500.

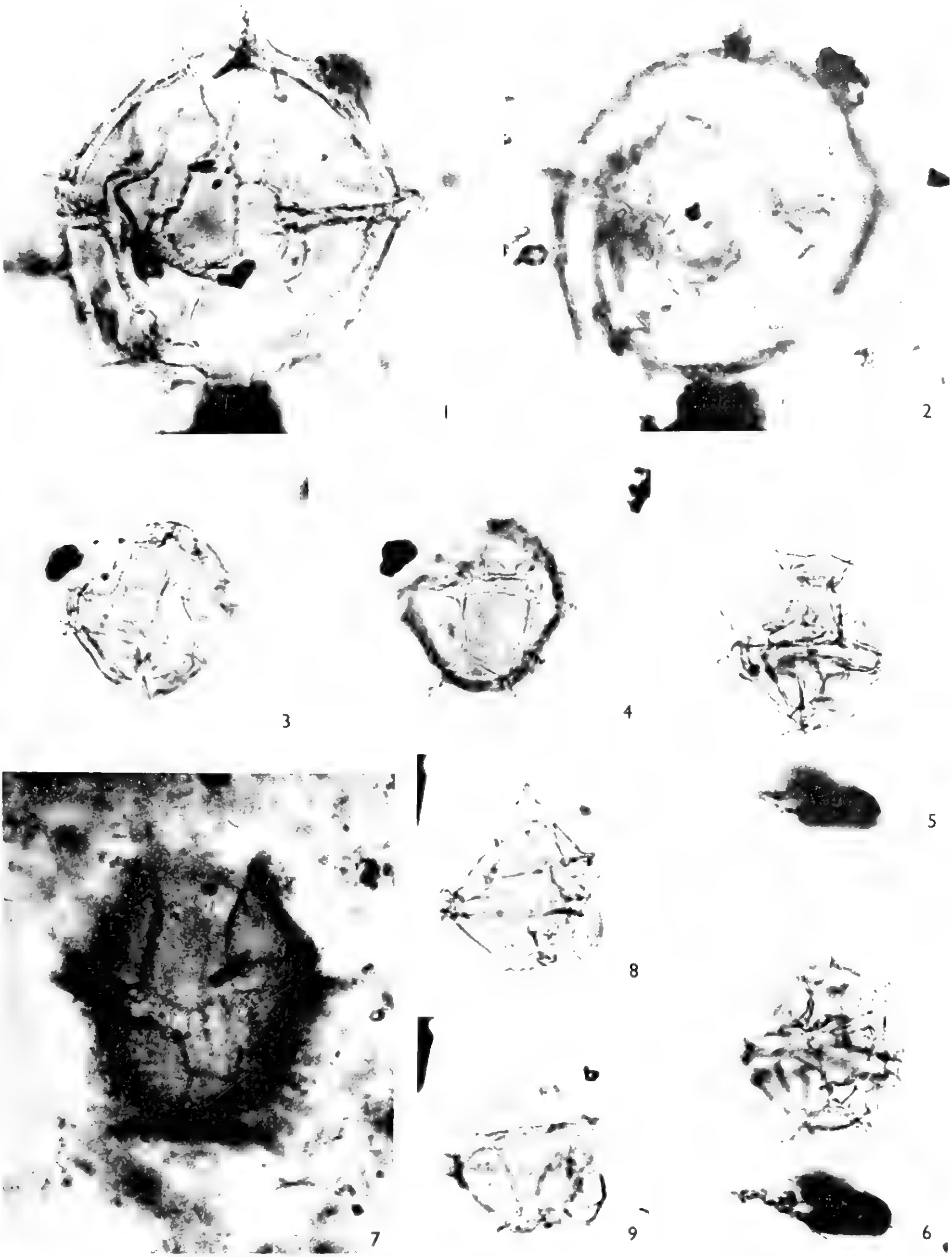

1
2
3
4
5
8
7
9
6

PLATE 16

Heliodinium patriciae Neale & Sarjeant

FIG. 1. The holotype, V.51710(1), in lateral view. Photographed by phase contrast. ×500.

Heliodinium voigti Alberti

FIG. 2. Ventral surface of specimen, PF.3035(4). ×500.

Microdinium* cf. *ornatum Cookson & Eisenack

FIG. 3. A rather large specimen, oblique ventral view. ×500.

FIG. 4. The same specimen in oblique dorsal view, by transparency. ×500.

FIG. 5. Ventral surface of specimen, PF.3050(1). ×500.

FIG. 6. Dorsal surface of same specimen, viewed by transparency. ×500.

Hystrichodinium pulchrum Deflandre

FIG. 7. Dorsal view of specimen V.51737(1). ×500.

FIG. 8. Lateral view of specimen, V.51737(2), showing archaeopyle. ×500.

Microdinium setosum sp. nov.

FIG. 9. Ventral surface of holotype, PF.3046(2). ×500.

FIG. 10. Dorsal surface of same, viewed by transparency. ×500.

Xiphophoridium alatum (Cookson & Eisenack)

FIG. 11. Antapical view of specimen. PF.3051(1). ×500.

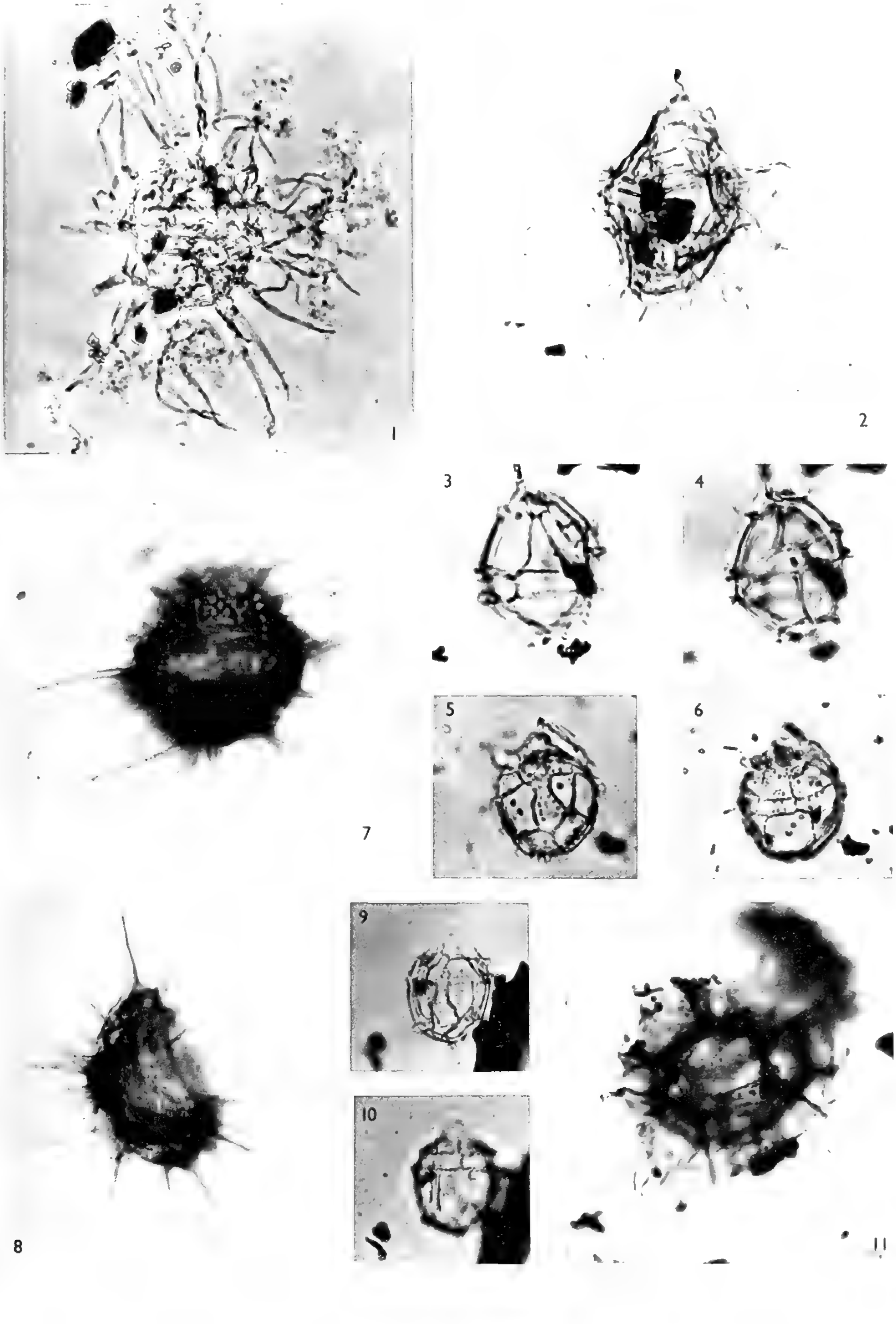

1
2
3
4
5
6
7
8
9
10
11

PLATE 17

Hystrichokolpoma eisenacki sp. nov.

FIG. 1. Specimen showing the long antapical process, the slender equatorial processes and the deep sulcal notch. V.51753(2). ×660.

FIG. 2. Holotype, V.51958(1). ×660.

FIG. 3. Specimen with apical plates in position. V.51752(4). ×400.

Hystrichokoploma rigaudae Deflandre & Cookson

FIG. 4. Precingular, equatorial, and postcingular and antapical processes are clearly visible. V.51757(2). ×400.

Hystrichokolpoma eisenacki var. ***turgidum*** nov.

FIG. 5. Holotype. V.51959(1). ×400.

Hystrichokolpoma unispinum sp. nov.

FIG. 6. Specimen with all processes buccinate. V.51960(1). ×660.

FIG. 7. Holotype. Apical view, sulcus marked by belt of small pores at top left. V.51961(1). ×660.

PLATE 17

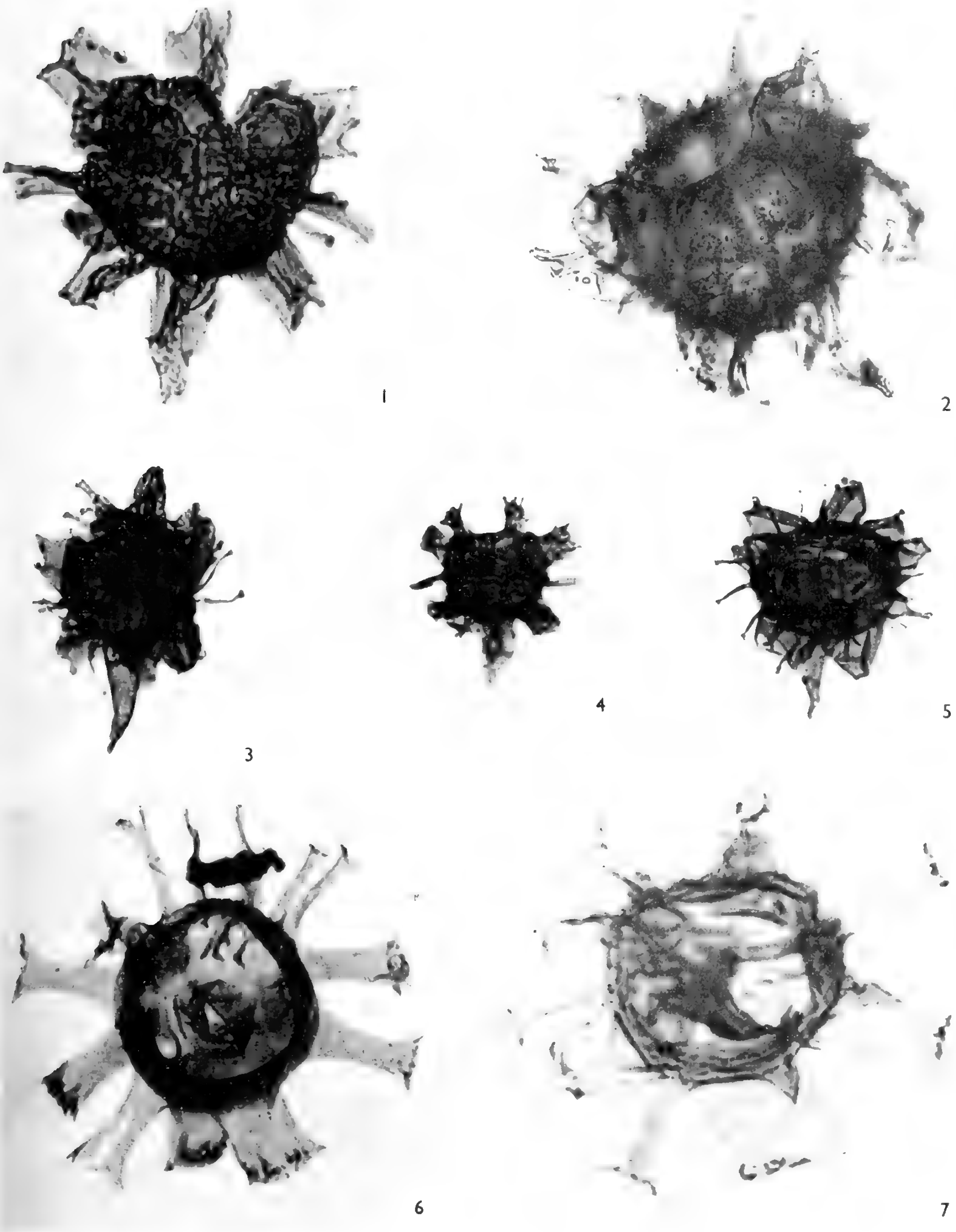


PLATE 18

Wetzeliella (Wetzeliella) articulata Eisenack

FIG. 1. Specimen dorsal side uppermost showing archaeopyle, dorsal view. V.51955(2). ×330.

FIG. 2. Specimen, ventral side uppermost. V.51961(1). ×330.

FIG. 3. Isolated periphragm operculum from archaeopyle of outer shell. Processes, except for central use, arranged in simulate complexes. V.51763(2). ×700.

FIG. 4. Isolated endophragm operculum from archaeopyle of inner body. V.51763(2). ×700.

Wetzeliella (Wetzeliella) articulata var. **_conopia_** nov.

FIG. 5. Specimen, dorsal side uppermost, with periphragm archaeopyle. Slightly displaced. V.51962. ×330.

Wetzeliella (Wetzeliella) clathrata Eisenack

FIG. 6. Narrow strips of minutely perforate membrane connect the distal ends of the processes. V.51958(2). ×330.

Wetzeliella (Wetzeliella) homomorpha var. **_quinquelata_** nov.

FIG. 7. Specimen showing restriction of processes on the dorsal side to the simulate complexes. Periphragm operculum slightly displaced. V.51963(1). ×330.

Wetzeliella (Wetzeliella) coleothrypta sp. nov.

FIG. 8. Holotype. Ventral view. V.51753(3). ×330.

FIG. 9. Specimen with more numerous spines. V.51964(1). ×330.

Wetzeliella (Wetzeliella) ovalis Eisenack

FIG. 10. Dorsal view of specimen with operculum slightly displaced. V.51965(1). ×330.

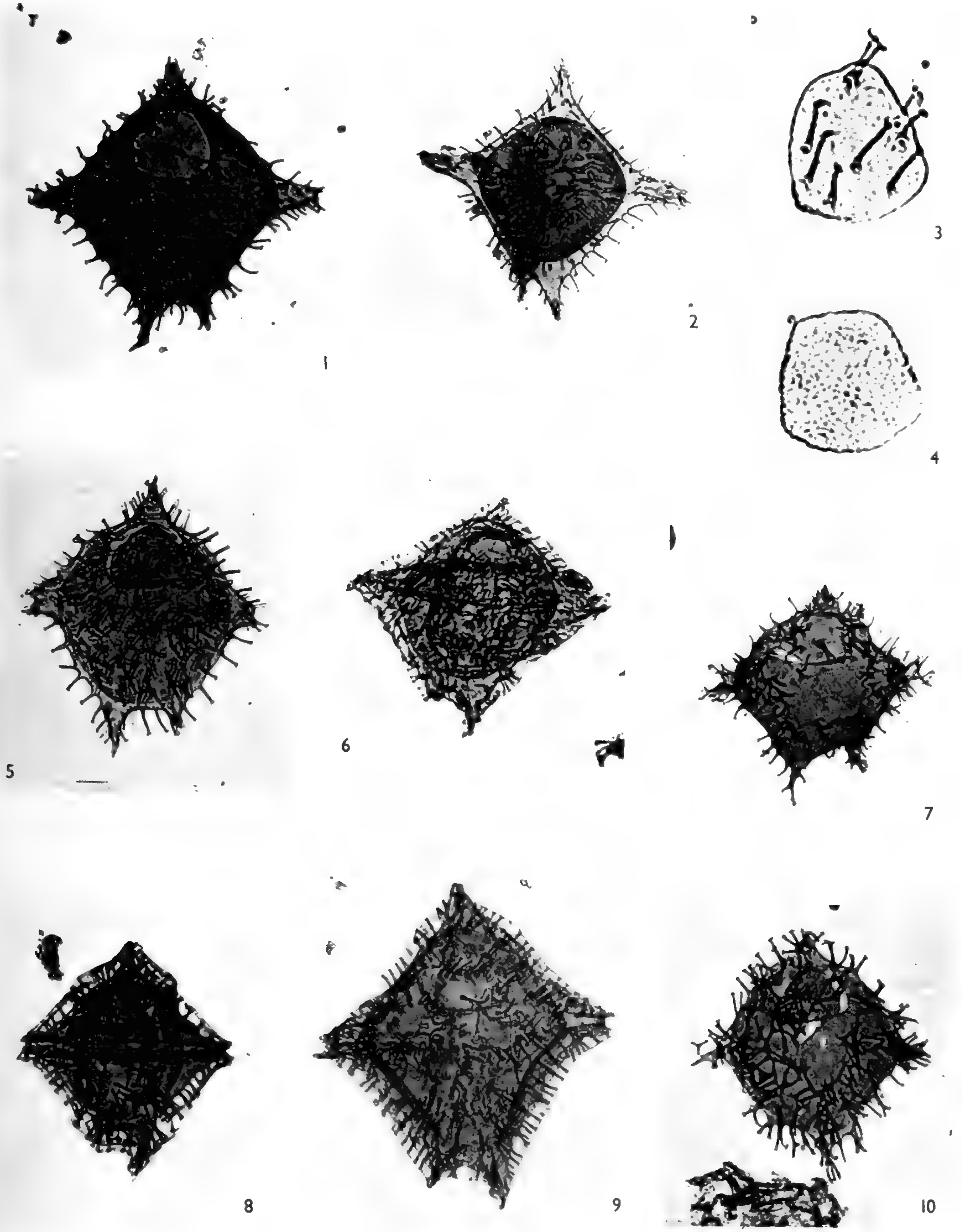

1
2
3
4
5
6
7
8
9
10

PLATE 19

Wetzeliella (Wetzeliella) tenuavirgula var. ***crassoramosa*** nov.

FIG. 1. Ventral view showing the simulate process complexes of plates 1′, 11″ and 7″. V.51966. ×1000.

FIG. 5. Dorsal view showing simulate complex of intercalary plate 2a, with thick linking bars. V.51966. ×1000.

FIG. 7. Ventral view, archaeopyle seen through ventral surface. Holotype. V.51954(2). ×500.

Wetzeliella (Wetzeliella) tenuivirgula sp. nov.

FIG. 2. Dorsal view of holotype with archaeopyle V.51964(2). ×330.

FIG. 4. Dorsal view showing periphragm archaeopyle formed by loss of plate 2a. Simulate complexes of plate 1a, 3a, 4″ and 5″ surround it. V.51752(5). ×1000.

Wetzeliella (Wetzeliella) reticulata sp. nov.

FIG. 3. Ventral view of holotype. V.51752(6). ×330

FIG. 6. Stimulate complex of plate 1′ and adjacent plates, showing distal network. V.51752 (6). ×1000.

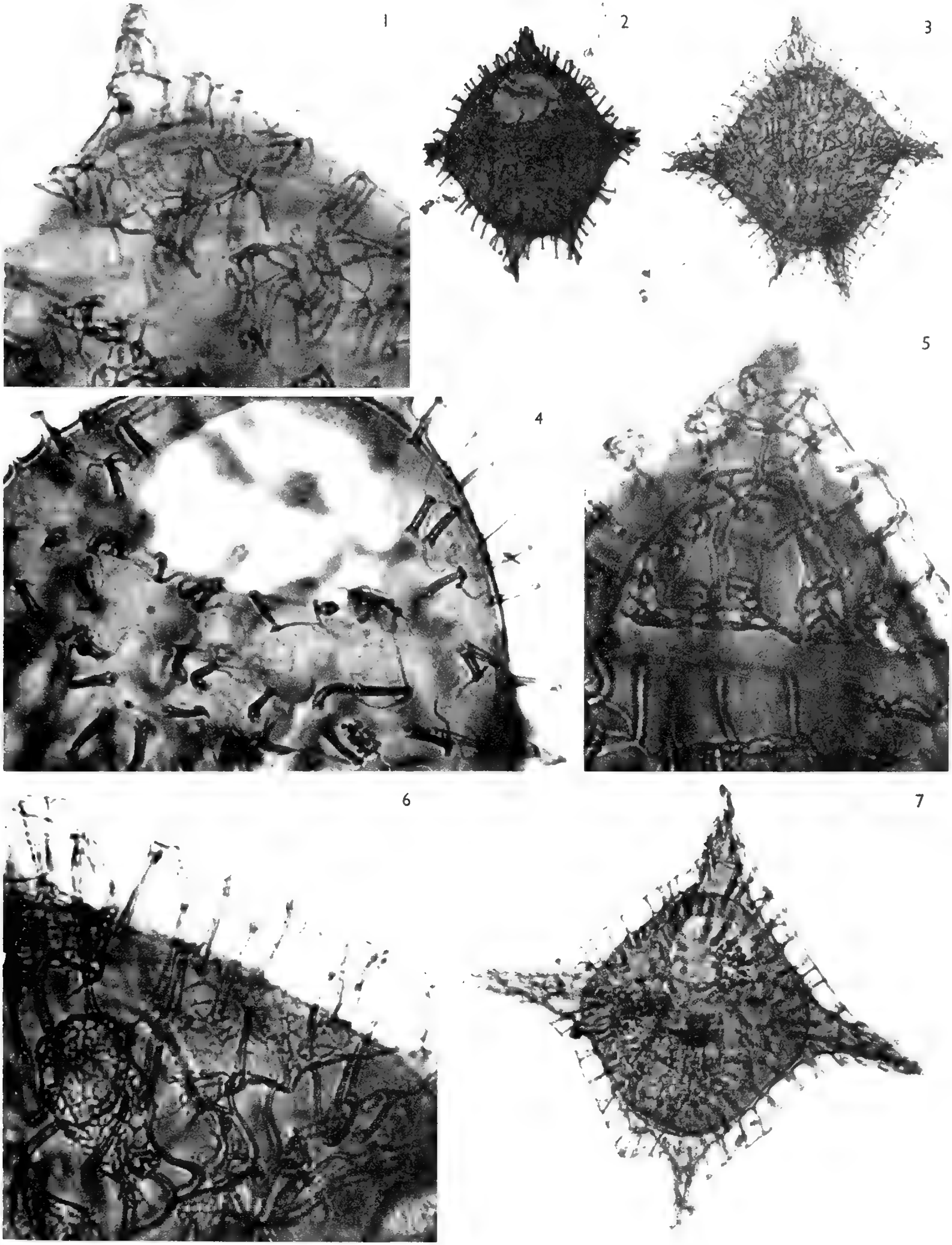

1
2
3
4
5
6
7

PLATE 20

Wetzeliella (Wetzeliella) condylos sp. nov.

FIG. 1. Ventral view of holotype. V.51967. ×500.

FIG. 2. Specimen with no apical horn. V.51752(7). ×500.

Wetzeliella (Wetzeliella) symmetrica var. ***lobisca*** nov.

FIG. 3. Ventral view. V.51970. ×330.

Wetzeliella (Wetzeliella) varielongituda sp. nov.

FIG. 4. Holotype. Dorsal view, with operculum slightly displaced. V.51973. ×330.

FIG. 8. Dorsal view, operculum inside inner body. V.51971. ×330.

Wetzeliella (Wetzeliella) similis Eisenack

FIG. 5. Specimen with pyrite crystals concentrated in the horns. V.51969. ×330.

Wetzeliella (Wetzeliella) symmetrica Weiler

FIG. 6. Dorsal view. V.51974. ×330.

Wetzeliella (Wetzeliella) solida (Gocht)

FIG. 7. Specimen with operculum lying within the central body. V.51968. ×330.

Wetzeliella (Rhombodinium) glabra Cookson

FIG. 9. Specimen with periphragm operculum in place. V.51958(3). ×500.

FIG. 10. Specimen with operculum missing. Periphragm has been colonized by fungi. V.51972. ×500.

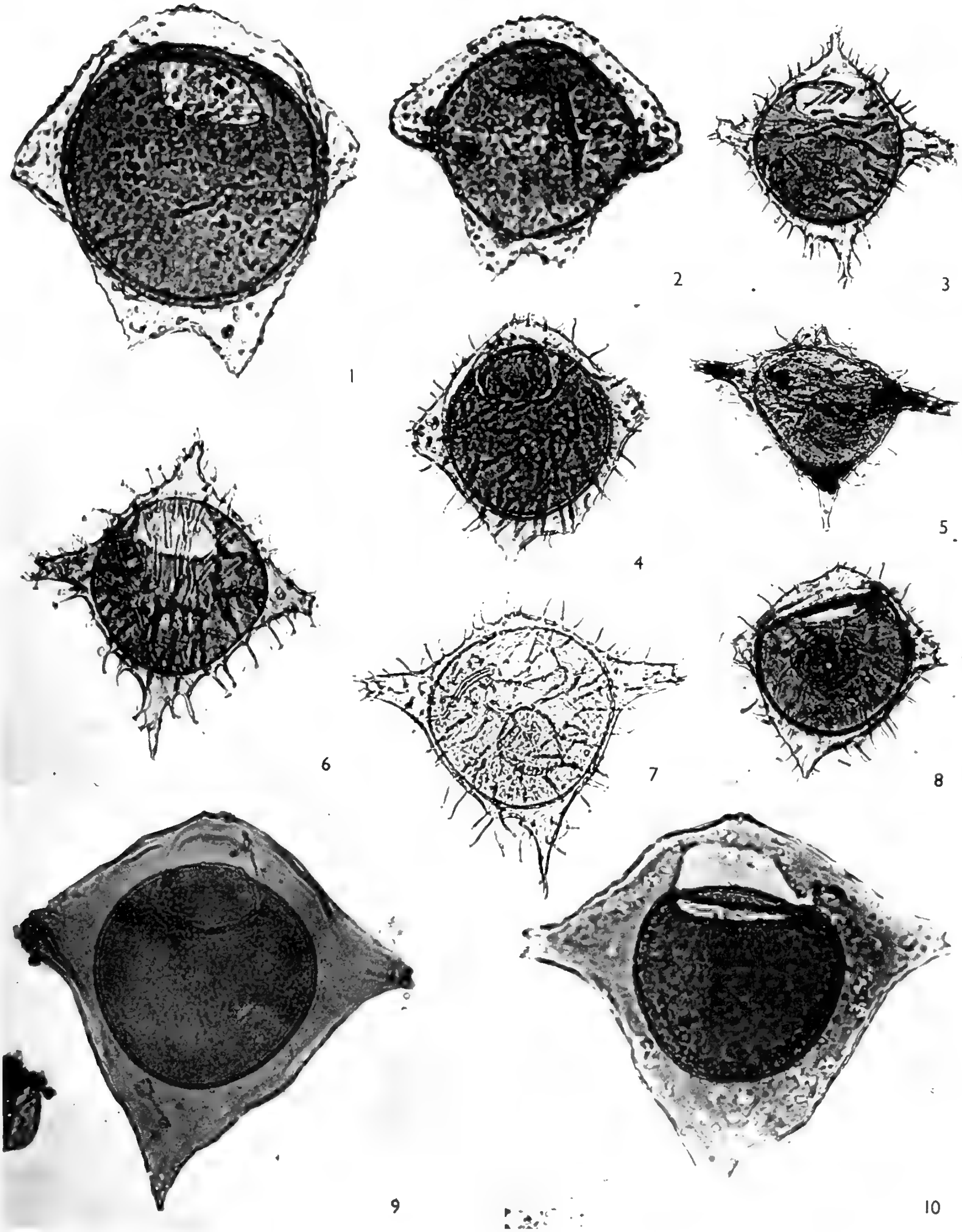

1
2
3
4
5
6
7
8
9
10

PLATE 21

?***Broomea longicornuta*** Alberti

FIG. 1. Specimen V.51733(1). ×500.

Odontochitina operculata (O. Wetzel)

FIG. 2. Specimen V.51730(4). ×c.400.

?***Dingodinium albertii*** sp. nov.

FIG. 3. Holotype, V.51719(2). ×500.

Gardodinium eisenacki Alberti

FIG. 4. Specimen V.51726(1). ×500.

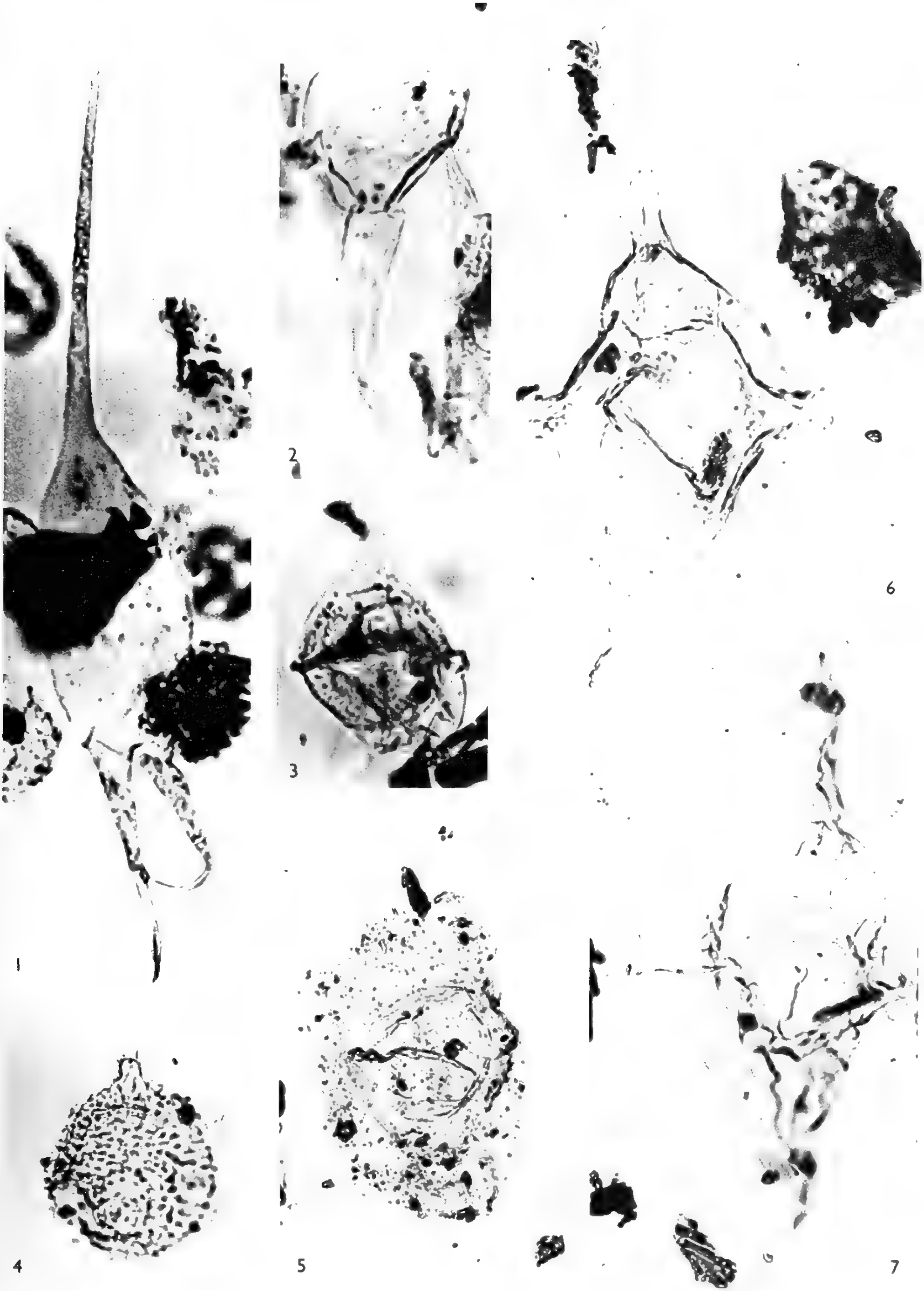
Paranetrelytron strongylum gen. et sp. nov.

FIG. 5. Holotype, V.51722(1). ×500.

Muderongia staurota sp. nov.

FIG. 6. Holotype, V.51724(3). ×650.

FIG. 7. Paratype, V.51718(3). ×650.



1
2
3
4
5
6
7

PLATE 22

Apteodinium maculatum Eisenack & Cookson

FIG. 1. Specimen V.51718(4). ×650.

Heslertonia heslertonense (Neale & Sarjeant)

FIG. 2. Specimen V.51724(2). ×500.

Netrelytron trinetron sp. nov.

FIG. 3. Holotype, V.51729(1). ×650.

Fromea amphora Cookson & Eisenack

FIG. 4. Specimen V.51732(1). ×500.

Systematophora schindewolfi (Alberti)

FIG. 5. Specimen V.51721(1). ×500.

Cometodinium sp.

FIG. 6. Specimen V.51723(2). ×500.

Sirmiodinium grossi Alberti

FIG. 7. Specimen V.51722(2). ×500.

Doidyx anaphrissa gen. et sp. nov.

FIG. 8. Holotype, V.51723(3). ×750.

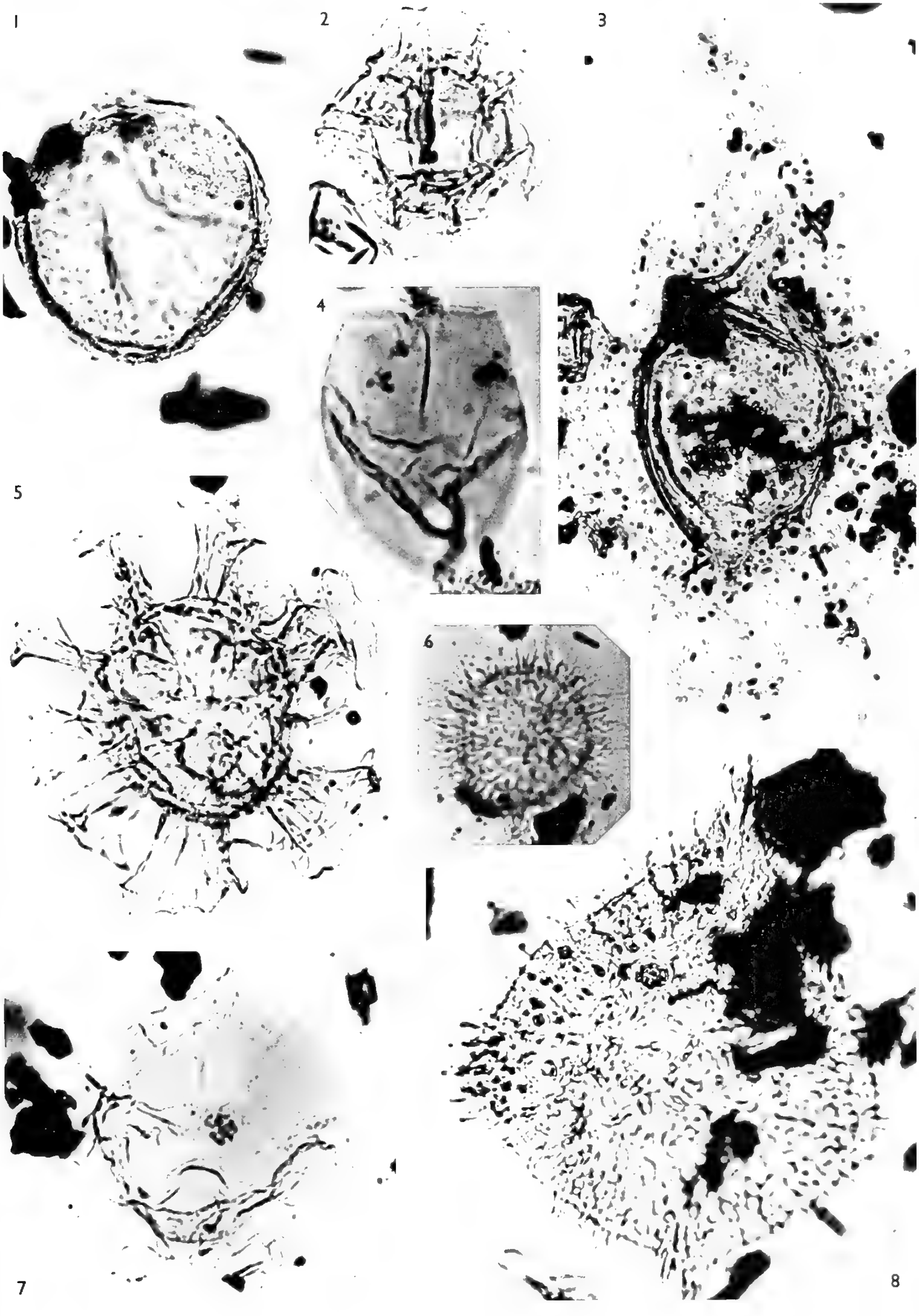

1
2
3
4
5
6
7
8

PLATE 23

?*Dingodinium albertii* sp. nov.

FIG. 1. Holotype, V.51719(2). highly magnified to show the tubercles. ×c.1250.

Pareodinia ceratophora Deflandre

FIG. 2. Specimen V.51724(4). ×500.

Fromea amphora Cookson & Eisenack

FIG. 3. Specimen V.51732(2). ×500.

Muderongia staurota sp. nov.

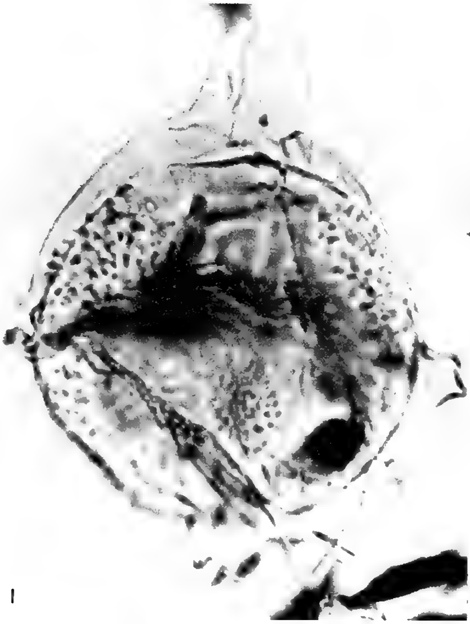
FIG. 4. Specimen V.51724(5), lacking the apex as a result of archaeopyle formation.

Paranetrelytron strongylum gen. et sp. nov.

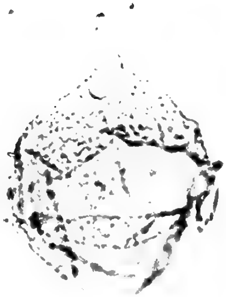
FIG. 5. Holotype, V.51722(1), photographed by phase contrast at high magnification to show the separation of endophragm from periphragm. ×c.1250.

Doidyx anaphrissa gen. et sp. nov.

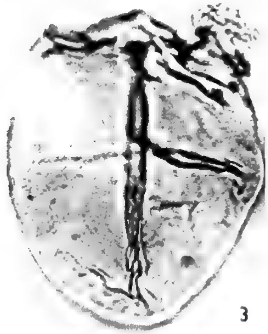
FIG. 6. Specimen V.51720(1), lacking the apex as a result of archaeopyle formation. ×500.



1



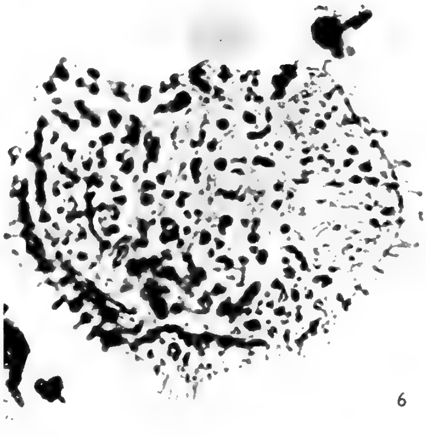
2



3

4

5



6

PLATE 24

?***Adnatosphaeridium patulum*** sp. nov.

FIG. 1. Specimen with archaeopyle. V.51975(2). ×330.

FIG. 2. Holotype Complete specimen. V.51977(1). ×330.

Adnatosphaeridium vittatum gen. et sp. nov.

FIG. 3. Complete specimen. V.51753(4). ×500.

FIG. 7. Holotype with apical archaeopyle. V.51976(1). ×500.

Membranilarnacia reticulata sp. nov.

FIG. 4. Holotype. V.51959(2). ×500.

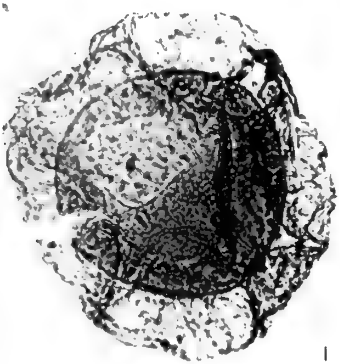
FIG. 6. Specimen with apical archaeopyle. V.51754(2). ×500.

Adnatosphaeridium multispinosum sp. nov.

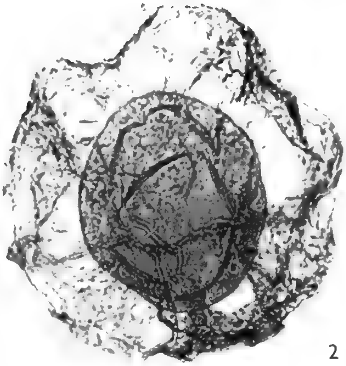
FIG. 5. Specimen with apical archaeopyle. V.51975(1). ×660.

Cannosphaeropsis reticulensis Pastiels

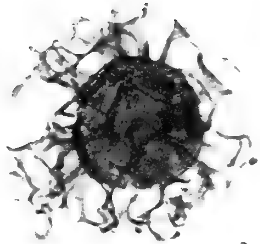
FIG. 8. Complete specimen. V.51964(3). ×500.



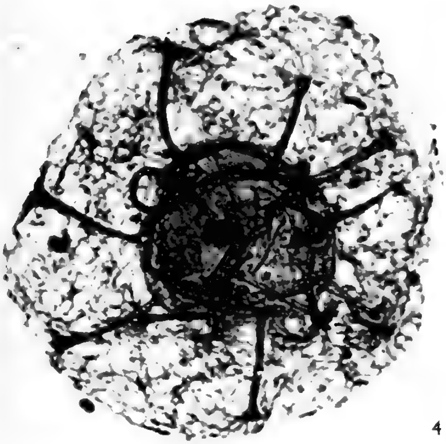
1



2



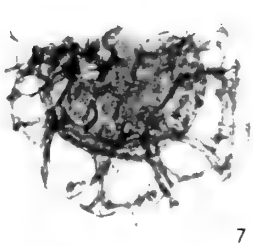
3



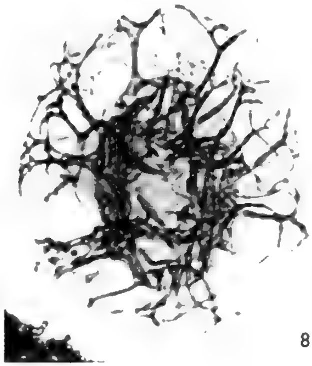
4

5

6



7



8

PLATE 25

Cyclonephelium divaricatum sp. nov.

FIG. 1. Specimen with apical archaeopyle and processes on all plates, V.51956(2). ×500.

Cyclonephelium pastielsi Deflandre & Cookson

FIG. 2. Specimen with operculum in place. V.51978(1). ×500.

Cyclonephelium ordinatum sp. nov.

FIG. 3. Dorsal view of specimen with apical archaeopyle. V.51977(2). ×330.

Areoligera cf. ***medusettiformis*** (O. Wetzel)

FIG. 4. Dorsal view of specimen with apical archaeopyle, note sulcal notch on the right of the mid-ventral line. V.51746(3). ×660.

Areoligera cf. ***coronata*** (O. Wetzel)

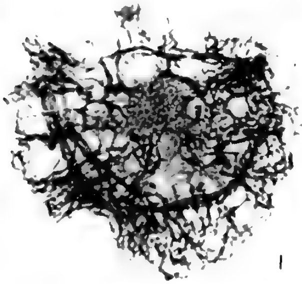
FIG. 5. Specimen showing the soleate process complexes on the ventral surface. V.51756(4). ×660.

Areoligera cf. ***senonensis*** Lejeune-Carpentier

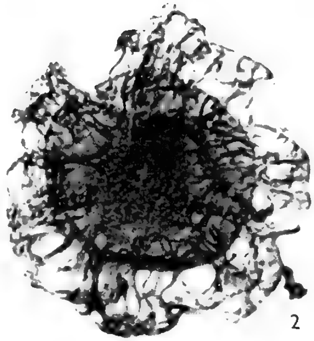
FIG. 6. Complete specimen. V.51757(3). ×660.

Areoligera coronata (O. Wetzel)

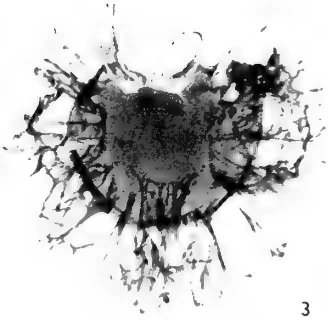
FIG. 7. Dorsal view. Processes arranged in soleate complexes, apical archaeopyle. V.51959 (3). ×500.



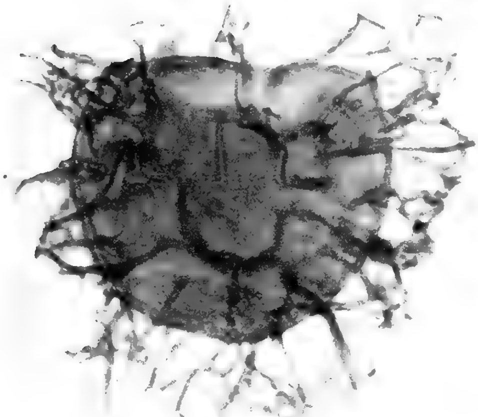
1



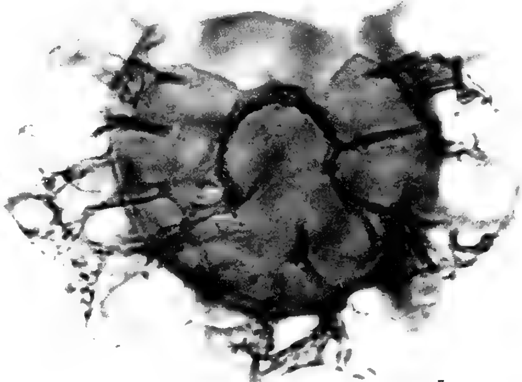
2



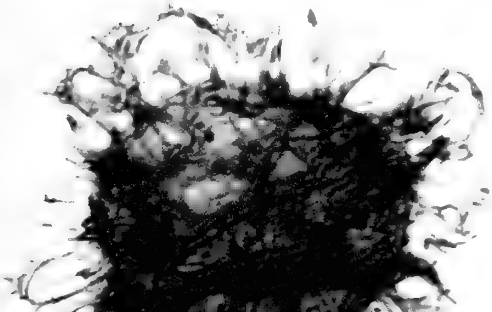
3



4



5



6

7

PLATE 26

Deflandrea oebisfeldensis Alberti

FIG. 1. Specimen with endrophragm operculum slightly displaced. V.51979. ×400.

Deflandrea phosphoritica subsp. ***phosphoritica*** Cookson & Eisenack

FIG. 2. Specimen with no inner body, periphragm operculum lying inside. V.51753(5). ×400.

FIG. 3. Specimen showing girdle and slightly displaced periphragm operculum. V.51955(3). ×400.

FIG. 6. Specimen with a "decomposed" inner body. V.51752(8). ×400.

FIG. 9. Specimen with archaeopyle. V.51747(3). ×400.

Deflandrea phosphoritica subsp. ***australis*** Cookson & Eisenack

FIG. 4. Complete specimen. V.51752(9). ×400.

Deflandrea wardensis sp. nov.

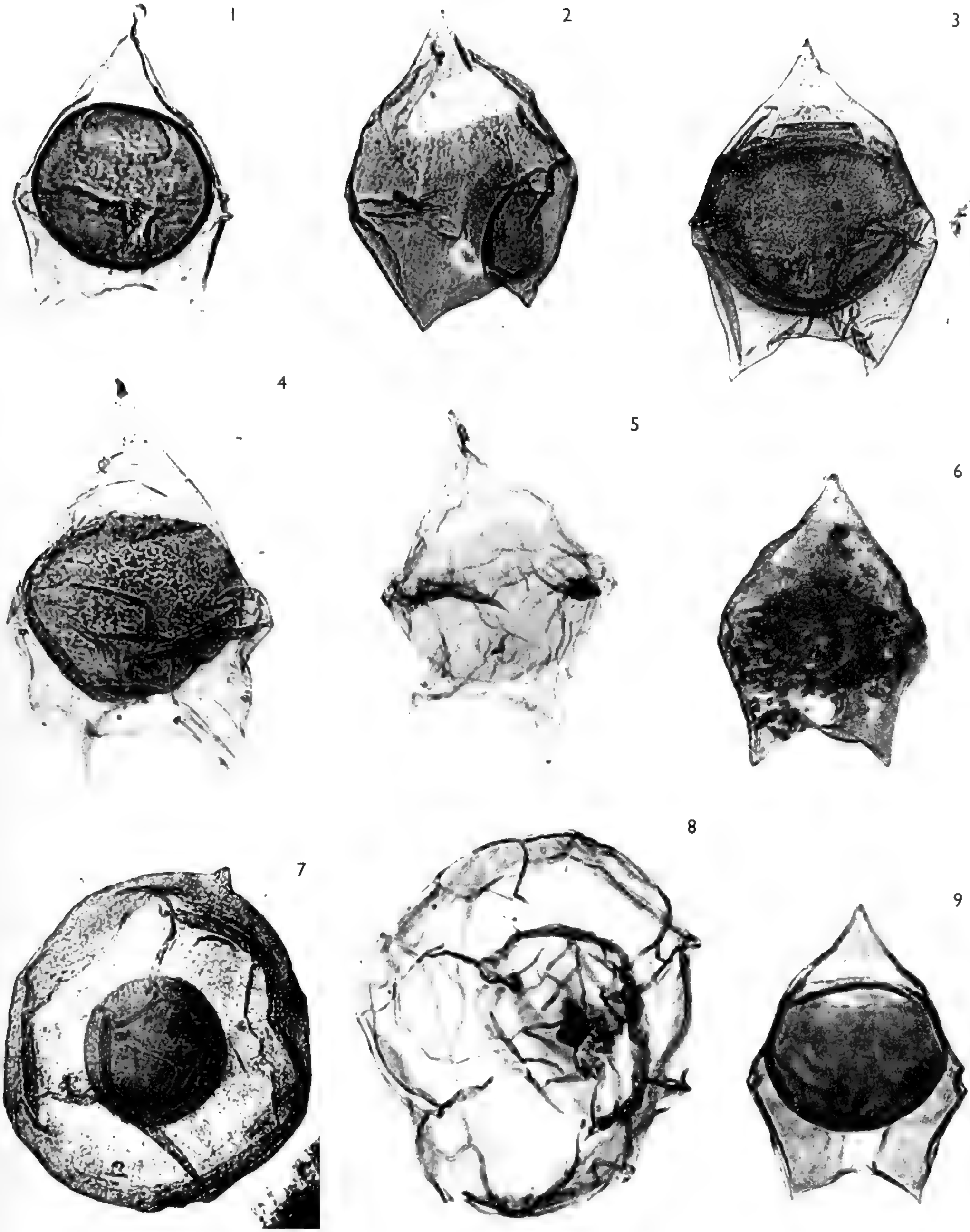
FIG. 5. Holotype with archaeopyle. V.51980(1). ×400.

Thalassiphora pelagica (Eisenack)

FIG. 7. An operculum is visible. V.51757(4). ×240.

Thalassiphora delicata sp. nov.

FIG. 8. Holotype. V.51756(3).


1
2
3
4
5
6
7
8
9

Printed in England by Staples Printers Limited at their Kettering, Northants, establishment

APPENDIX TO "STUDIES ON MESOZOIC AND CAINOZOIC DINOFLAGELLATE CYSTS"

R. J. DAVEY, C. DOWNIE,
W. A. S. SARJEANT, AND
G. L. WILLIAMS

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Appendix to Supplement No. 3
LONDON: 1969

APPENDIX TO "STUDIES ON MESOZOIC AND CAINOZOIC DINOFLAGELLATE CYSTS"

BY

ROGER JACK DAVEY,

CHARLES DOWNIE,
(University of Sheffield)

WILLIAM ANTONY SWITHIN SARJEANT,
(University of Nottingham)

AND GRAHAM LEE WILLIAMS
(Pan-American Petroleum Corp.)

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Appendix to Supplement 3
LONDON: 1969

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

In 1965 *a separate supplementary series of longer papers was instituted, numbered serially for each Department.*

This paper is Appendix to Supplement No. 3 *of the Geological (Palaeontological) series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

World List abbreviation
Bull. Br. Mus. nat. Hist. (Geol.) Suppl.

© Trustees of the British Museum (Natural History) 1969

TRUSTEES OF THE
BRITISH MUSEUM (NATURAL HISTORY)

Issued 11 *December,* 1969

Price Sixteen Shillings
(£0·80)

APPENDIX TO "STUDIES ON MESOZOIC AND CAINOZOIC DINOFLAGELLATE CYSTS"

By ROGER JACK DAVEY, CHARLES DOWNIE,
WILLIAM ANTONY SWITHIN SARJEANT, AND
GRAHAM LEE WILLIAMS

Manuscript accepted October 1968

CONTENTS

SYNOPSIS

This Appendix comprises taxonomic revisions necessary to correct inadvertent errors in the Supplement and to take account of subsequent taxonomic studies. The diagnoses of two genera, *Gonyaulacysta* and *Leptodinium*, are emended ; a new genus, *Hystrichogonyaulax*, and two new species, *Perisseiasphaeridium eisenackii* and *Polysphaeridium belgicum*, are proposed ; and revisions in the generic assignation of 114 other species are proposed. Typographical errors are corrected and curatorial amendments are incorporated.

I. INTRODUCTION

In a lengthy review (1967 ; 1030–3), Tappan & Loeblich Jnr. have noted that the new combinations resulting from generic reallocations proposed in our supplement in many instances failed to fulfil the requirements of Article 33, para. 4 of the " International Code of Botanical Nomenclature " (1961 edition, then applicable).

This Appendix attempts to set these matters right. In sections II–V taxonomic reallocations are proposed ; in section VI, taxonomic reallocations by other authors are noted with comments; and in section VII, typographical and phraseological errors in the original work (some of them noted by the reviewers, others noted by the authors) are corrected and certain curatorial amendments to the numbering of specimens are listed. New species and new combinations which were validly published in the original work are not again listed here.

The authors gratefully acknowledge helpful comments received from Dr. William R. Evitt (Stanford University, California) and Dr. Alfred R. Loeblich Jnr. (Chevron Research Company, La Habra, California). The work by W. A. S. Sarjeant was done whilst Visiting Professor at the University of Oklahoma, Norman, Oklahoma, U.S.A.: he would like to express personal thanks to Dr. Charles J. Mankin for his support and encouragement.

II. GENERIC REALLOCATIONS (R.J.D. & G.L.W.)

Achomosphaera alcicornu (Eisenack) Davey & Williams, comb. nov., =*Hystrichosphaeridium alcicornu* Eisenack, 1954 ; 65–6, pl. 10 figs 1–2, text-fig. 5. Oligocene, East Prussia, U.S.S.R.

Achomosphaera grallaeforme (Brosius) Davey & Williams, comb. nov., =*Hystrichosphaeridium grallaeforme* Brosius, 1963 ; 42 pl. 5 fig. 3, text-fig. 2 nos. 3 a–b. Oligocene, Germany.

Achomosphaera hyperacantha (Deflandre & Cookson) Davey & Williams, comb. nov., =*Hystrichosphaera hyperacantha* Deflandre & Cookson, 1955 ; 264–5, pl. 6 fig. 7. Miocene, Australia.

Achomosphaera hirundo (Eisenack) Davey & Williams, comb. nov., =*Hystrichosphaeridium hirundo* Eisenack, 1958 ; 404–5, pl. 24 fig. 12. Lower Cretaceous, Germany.

Achomosphaera triangulata (Gerlach) Davey & Williams, comb. nov., =*Baltisphaeridium triangulatum* Gerlach, 1961 ; 194–5, pl. 29 fig. 1. Miocene, Germany.

Cymatiosphaera membranacea (Philippot) Davey & Williams, comb. nov., =*Hystrichosphaeridium membranaceum* Philippot, 1949 ; 57–8, text-fig. 3. Upper Cretaceous, France. (Acritarch).

?Hystrichokolpoma xiphea (Maier) Davey & Williams, comb. nov., =*Galea xiphea* Maier 1959 ; 309, pl. 30 fig. 5 (transferred to *Hystrichosphaeridium* by Sarjeant, 1964 ; 176). Oligocene, Germany.

Hystrichosphaera leptoderma (Maier) Davey & Williams, comb. nov., =*Hystrichosphaeridium leptodermum* Maier, 1959 ; 321–2, pl. 33 figs. 5–6. Oligocene, Germany.

Oligosphaeridium albertense (Pocock) Davey & Williams, comb. nov., =*Hystrichosphaeridium albertense* Pocock, 1962 ; 82, pl. 15 figs. 226–7. Lower Cretaceous, Alberta, Canada.

?Oligosphaeridium asterigerum (Gocht) Davey & Williams, comb. nov., =*Hystrichosphaeridium asterigerum* Gocht, 1959 ; 67–8, pls. 3 fig. 1, 7 figs. 1–3. Lower Cretaceous, Germany.

?Oligosphaeridium coelenteratum (Tasch) Davey & Williams, comb. nov., =*Hystrichosphaeridium coelenteratum* Tasch *in* Tasch, McClure & Oftedahl, 1964 ; 195, pl. 2 fig. 11. Lower Cretaceous, Kansas, U.S.A.

Oligosphaeridium dictyophorum (Cookson and Eisenack) Davey & Williams, comb. nov., =*Hystrichosphaeridium dictyophorum* Cookson & Eisenack, 1958 ; 44, pl. 11 fig. 14. Upper Jurassic, Papua.

?Oligosphaeridium dispare (Tasch) Davey & Williams, comb. nov., =*Hystrichosphaeridium dispare* Tasch *in* Tasch, McClure & Oftedahl, 1964 ; 195, pl. 2 fig. 8. Lower Cretaceous, Kansas, U.S.A.

?Oligosphaeridium irregulare (Pocock) Davey & Williams, comb. nov., =*Hystrichosphaeridium irregulare* Pocock, 1962 ; 82–3, pl. 15 figs. 228–9, *non Hystrichosphaeridium irregulare* (Merrill) Sarjeant, 1964. [The holotype of this latter species, originally described (as ?*Geodia irregularis*) from the Middle Cretaceous of Texas, U.S.A., is lost ; it is considered to be a junior synonym of *Hystrichosphaeridium complex* (White, 1842) Deflandre, 1946b, by Sarjeant, 1966a ; 8]. Lower Cretaceous, Alberta, Canada.

?Oligosphaeridium paradoxum (Brosius) Davey & Williams, comb. nov., =*Hystrichosphaeridium paradoxum* Brosius, 1963 ; 41–2, pl. 4 fig. 6, text-fig. 2, nos. 1a–c. Oligocene, Germany.

Oligosphaeridium perforatum (Gocht) Davey & Williams, comb. nov., =*Hystrichosphaeridium perforatum* Gocht, 1959 ; 68–9, pls. 3 fig. 7 ; 7 figs. 13–16. Lower Cretaceous, Germany.

?Litosphaeridium crassipes (Reade) Davey & Williams, comb. nov., =*Xanthidium crassipes* Reade, 1839 ; pl. 9 figs. 2–5. (Transferred to *Hystrichosphaeridium* by Lejeune-Carpentier, 1941 ; 79–80). Upper Cretaceous, England.

?Litosphaeridium flosculus (Deflandre) Davey & Williams, comb. nov., =*Hystrichosphaeridium flosculus* Deflandre, 1937 ; 75–6, pl. 15 figs. 5–6. Upper Cretaceous, France.

?***Litosphaeridium truncigerum*** (Deflandre) Davey & Williams, comb. nov., =*Hystrichosphaeridium truncigerum* Deflandre, 1937 ; 71–2, pl. 13 figs. 6–7. Upper Cretaceous, France.

?***Cordosphaeridium cantharellum*** (Brosius) Davey & Williams, comb. nov., =*Hystrichosphaeridium cantharellum* Brosius, 1963 ; 40–1, pl. 6 fig. 1, text-fig. 2 nos. 11a–c. Oligocene, Germany.

?***Cordosphaeridium erectum*** (Manum & Cookson) Davey & Williams, comb. nov., =*Hystrichosphaeridium erectum* Manum & Cookson, 1964 ; 14, pl. 3 figs. 5–6. Cretaceous, Arctic Canada.

Perisseiasphaeridium eisenackii Davey & Williams, sp. nov., =*Hystrichosphaeridium anthophorum* sensu Eisenack, 1958 ; 402, pl. 26 figs. 1–2 *non* Cookson & Eisenack, 1958. Holotype : the specimen figured by Eisenack, 1958 ; pl. 26 fig. 1, and contained in his Slide Ob. Apt. no. 31. Dimensions of holotype : diameter of central body 55μ, overall diameter 110μ. Lower Cretaceous (Upper Aptian), Germany. (Name originally proposed by Davey & Williams, 1966b ; 79 : invalid under Art. 37, since the holotype was not designated).

?***Polysphaeridium asperum*** (Maier) Davey & Williams, comb. nov., =*Hystrichosphaeridium asperum* Maier, 1959 ; 319: pl. 33 fig. 2. Miocene, Germany.

?***Polysphaeridium deflandrei*** (Valensi) Davey & Williams, comb. nov., =*Hystrichosphaeridium deflandrei* Valensi, 1947 ; 817–8, text-fig. 3. Middle Jurassic France.

?***Polysphaeridium fabium*** (Tasch) Davey & Williams, comb. nov., =*Hystrichosphaeridium fabium* Tasch, *in* Tasch, McClure & Oftedahl, 1964 ; 195, pl. 2 fig. 5. Lower Cretaceous, Kansas, U.S.A.

?***Polysphaeridium follium*** (Tasch) Davey & Williams, comb. nov., =*Hystrichosphaeridium follium* Tasch, *in* Tasch, McClure & Oftedahl, 1964 ; 195, pl. 1 fig. 8. Lower Cretaceous, Kansas, U.S.A.

?***Polysphaeridium fucosum*** (Valensi) Davey & Williams, comb. nov., =*Micrhystridium fucosum* Valensi, 1955a ; 40, text-fig. 2b (Transferred to *Hystrichosphaeridium* by Downie and Sarjeant, 1963 ; 93). Cretaceous, France.

?***Polysphaeridium major*** (Lejeune-Carpentier) Davey & Williams, comb. nov., =*Hystrichosphaeridium major* Lejeune-Carpentier, 1940 ; 220–1, text-fig. 13. Upper Cretaceous, Belgium.

?***Polysphaeridium marsupium*** (Tasch) Davey & Williams, comb. nov., =*Hystrichosphaeridium marsupium* Tasch, *in* Tasch, McClure & Oftedahl, 1964 ; 193, pl. 3 fig. 16. Lower Cretaceous, Kansas, U.S.A.

?***Polysphaeridium paulinae*** (Valensi) Davey & Williams, comb. nov., =*Micrhystridium paulinae* Valensi, 1953 ; 48, pl. 12 fig. 6 (Transferred to *Hystrichosphaeridium* by Downie and Sarjeant, 1963 ; 93). Middle Jurassic, France.

?***Polysphaeridium perovatum*** (Tasch) Davey & Williams, comb. nov., =*Hystrichosphaeridium perovatum* Tasch, *in* Tasch, McClure & Oftedahl, 1964 ; 194, pl. 3 fig. 13. Lower Cretaceous, Kansas, U.S.A.

?Polysphaeridium rhabdophorum (Valensi) Davey & Williams, comb. nov., =*Hystrichosphaeridium rhabdophorum* Valensi, 1955b ; 593–4, pl. 3 fig. 7. Cretaceous, France.

?Polysphaeridium simplex (White) Davey & Williams, comb. nov., =*Xanthidium tubiferum* subsp. *simplex* White, 1842 ; 38–9, pl. 4 div. 3 fig. 10 (elevated to specific status, as *Hystrichosphaeridium simplex*, by Deflandre, 1946a ; card 934). Upper Cretaceous, England.

?Polysphaeridium tribrachiosum (Tasch) Davey & Williams, comb. nov., =*Hystrichosphaeridium tribrachiosum* Tasch *in* Tasch, McClure & Oftedahl, 1964 ; 195, pl. 1 fig. 3. Lower Cretaceous, Kansas, U.S.A.

?Diphyes monstruosum (Tasch) Davey & Williams, comb. nov., =*Hystrichosphaeridium monstruosum* Tasch *in* Tasch, McClure & Oftedahl, 1964 ; 195, pl. 1 fig. 12. Lower Cretaceous, Kansas, U.S.A.

Tanyosphaeridium ellipticum (Cookson) Davey & Williams, comb. nov., =*Hystrichosphaeridium ellipticum* Cookson, 1965 ; 87–8, pl. 11 figs. 1–3a. Upper Eocene, Australia.

Tanyosphaeridium isocalamus (Deflandre & Cookson) Davey & Williams, comb. nov., =*Hystrichosphaeridium isocalamus* Deflandre & Cookson, 1955 ; 272, pl. 2 figs 7–8, text-figs 30–35. Lower Cretaceous, Australia.

III. TAXONOMIC CHANGES PROPOSED BY W. A. S. SARJEANT

In a recent publication, Wall (1967 ; 98) has discussed the difficulties encountered in distinguishing between the genera *Gonyaulacysta* and *Leptodinium*. Hitherto this had been done on the presence of a sixth precingular plate (numbered as plate 1''') in the former genus—a feature frequently difficult to discern, even in the type species, *G. jurassica*. Wall proceeded to formulate a revised diagnosis for the genus *Leptodinium*, emphasizing the absence of apical or antapical structures and the simplicity of the crests, which are typically low and lack spines or other outgrowths (1967 ; 104). This diagnosis did not take account of the revisions in these two genera proposed by Sarjeant (1966b ; 111, 113) ; and so revised diagnoses for the genera *Gonyaulacysta* and *Leptodinium*, embodying ideas drawn from both sources, are now given. Two species which fall outside the revised diagnoses of both genera are placed into a new genus, here proposed.

Genus *GONYAULACYSTA* Deflandre ex Norris & Sarjeant 1965 emend, Sarjeant, herein

1964 *Gonyaulacysta* gen. nov. Deflandre : 5. [Type species not validly proposed : see I.C.B.N. Art. 33 para. 4].
1965 *Gonyaulacysta* Deflandre ; Norris and Sarjeant : 65. [Type species validly proposed].
1966 *Gonyaulacysta* Deflandre ; Loeblich & Loeblich : 33.
1966b *Gonyaulacysta* Deflandre ; emend. Sarjeant : 111.
1967 *Gonyaulacysta* Deflandre ; Wall : 98 (discussion only : no diagnosis given).

Emended diagnosis. Proximate dinoflagellate cysts, spherical, ovoidal, ellipsoidal or polyhedral, with an apical horn and the reflected tabulation 3–4′, 0–1a, 6″, 6c, 5–6‴, 1 p, 0–1 p.v., 1⁗, 0–x s. Cingulum strongly or weakly helicoid ; cingular plates well or poorly marked. Sulcus generally but not constantly extending on to the epitract ; undivided or subdivided into a variable number of small plates. Apical horn typically formed from the periphragm only, less frequently from both shell layers ; rarely, an apical or antapical pericoel is present (but not both), but the two layers are most often otherwise in continuous contact. Median and antapical horns lacking. Sutures marked by low ridges ; bearing crests of varied form (smooth, denticulate or spinous, perforate or imperforate) ; or marked by lines of spines of varied form. Height of spines or crests always less than $\frac{1}{4}$ of shell width. A precingular single-plate archaeopyle, formed by loss of plate 3″, is developed, the operculum typically becoming wholly detached : in some individual specimens, the archaeopyle may not be developed. Surface of periphragm smooth, granular, nodose, punctate or reticulate ; forms with a general spine cover are excluded.

Type species. *Gonyaulacysta jurassica* (Deflandre) Norris & Sarjeant, 1965 =*Gonyaulax jurassica* Deflandre, 1938 ; 168–70, pl. 6 figs. 2–5, text-figs. 1–2. Upper Jurassic (Oxfordian), France.

Remarks. The diagnosis is emended to include the presence of an apical horn, formed by an outbulge of the periphragm or of both shell layers, as an essential characteristic. Species in which an apical prominence is developed merely from the junction of crests, such as *Leptodinium freakei* (Sarjeant) Sarjeant and *Leptodinium millioudi* (Sarjeant) Sarjeant, are excluded, as are species with a general spine cover or with especially long sutural spines (see discussion in Sarjeant, 1966b ; 111). Species having an apical or epitractal archaeopyle, species having a precingular archaeopyle formed by the loss of the equivalent of more than one plate, and species having a combination archaeopyle are excluded. The currently known range of the genus is Middle Jurassic—Miocene.

Other species.

Gonyaulacysta aculeata (Klement) Sarjeant, comb. nov., =*Gonyaulax aculeata* Klement, 1960 ; 42–4, pl. 5 figs. 6–9, text-fig. 21. Upper Jurassic, Germany.

Gonyaulacysta aichmetes Sarjeant, 1966b ; 123–4, pl. 13 figs. 5–6, text-fig. 30. Lower Cretaceous, England.

Gonyaulacysta ambigua (Deflandre) Sarjeant, comb. nov. =*Gonyaulax ambigua* Deflandre, 1939 ; 144, pl. 6 fig. 2. Upper Jurassic, France.

(Note : The indirect citation of Deflandre's paper in Sarjeant 1968, does not conform to Art. 33 para. 3 and note 1 of the 'I.C.B.N.'. The new combination is, therefore, here reproposed.)

Gonyaulacysta apionis (Cookson & Eisenack) Sarjeant, comb. nov., =*Gonyaulax apionis* Cookson & Eisenack, 1958 ; 36, pl. 3 fig. 7, text-figs. 3–4. Lower Cretaceous, Australia.

Gonyaulacysta axicerastes Sarjeant, 1966b ; 114–6, pl. 13 figs. 11–12, text-fig. 25. Lower Cretaceous, England.

Gonyaulacysta cassidata (Eisenack & Cookson) Sarjeant, 1966b ; 125–6, pl. 14 figs. 3–4, text-fig. 31 =*Gonyaulax helicoidea* subsp. *cassidata* Eisenack & Cookson, 1960 ; 3, pl. 1, figs. 5–6. Lower Cretaceous, Australia.

Gonyaulacysta cladophora (Deflandre) Sarjeant, comb. nov., =*Gonyaulax cladophora* Deflandre, 1938 ; 173–6, pl. 7 figs. 1–5, text-figs. 5–6. Upper Jurassic, France.*

Gonyaulacysta confusa (Vozzhennikova) Sarjeant, comb. nov., =*Gonyaulax confusus* (sic) Vozzhennikova, 1967 : 80, pl. 17, figs. 1a,b ; pl. 25, figs. 4–5, pl. 27, figs. 3–4. Upper Jurassic, U.S.S.R.

Gonyaulacysta crassicornuta (Klement) Sarjeant, comb. nov., =*Gonyaulax crassicornuta* Klement, 1960 ; 38–9, pl. 5 figs. 1–3. Upper Jurassic, Germany.

Gonyaulacysta cretacea (Neale & Sarjeant) Sarjeant, comb. nov., =*Gonyaulax cretacea* Neale & Sarjeant, 1962 ; 441–3, pl. 19 figs. 1–2, text-fig. 2. Lower Cretaceous, England.

Gonyaulacysta crispa (W. Wetzel) Sarjeant, comb. nov., =*Conyaulax crispa* W. Wetzel 1966 ; 870, pl. 15, figs 4a–b. Middle Jurassic, Germany.

Gonyaulacysta dangeardi Sarjeant, 1968 ; 226–7, pl. 1 fig. 21, pl. 3 figs. 8, 15, text-fig. 3. Upper Jurassic, France.

Gonyaulacysta diaphanis (Cookson & Eisenack) Sarjeant, comb. nov., =*Gonyaulax diaphanis* Cookson & Eisenack, 1958 ; 36–7, pl. 3 figs. 13–14, text-figs. 10–11. Lower Cretaceous, Australia.

Gonyaulacysta dictyophora (Deflandre) Sarjeant, comb. nov., =*Palaeoperidinium dictyophorum* Deflandre, 1938 ; 178–9, pl. 8 figs. 1–3. [NOTE : Sarjeant, 1967 ; 249, formulated an emended diagnosis for this species and proposed its transfer to *Gonyaulacysta*. The generic transfer is, however, invalid in that the original place of publication cited was indirect (via the Downie & Sarjeant " Bibliography ") and not direct (I.C.B.N. Art 33 para. 1 and note 1). The emended diagnosis is considered applicable to this new combination.] Upper Jurassic, France.

Gonyaulacysta eisenacki (Deflandre 1938 ; 171–3, pl. 6 figs. 7–10, text-figs. 3–4) Sarjeant, 1968 ; 227, pl. 3 fig. 14. Upper Jurassic, France.

Gonyaulacysta episoma Sarjeant, 1966b ; 118–19, pl. 13 figs. 9–10, text-fig. 27. Lower Cretaceous, England.

Gonyaulacysta exilicristata Davey, 1968a ; 121, pl. 1, figs. 1–2, text-figs. 9A–B. Upper Cretaceous, England.

Gonyaulacysta fetchamensis Sarjeant 1966b ; 128–30, pl. 15 figs. 1–2, text-fig. 33. Upper Cretaceous, England.

Gonyaulacysta giuseppei (Morgenroth) Sarjeant, comb. nov., =*Gonyaulax giuseppei* Morgenroth, 1966 ; 5–6, pl. 2 figs. 3–6. Eocene, Germany.

Gonyaulacysta gongylos Sarjeant, 1966b ; 111–13, pl. 13 figs. 1–2, text-fig. 23. Upper Jurassic, England.

Gonyaulacysta gottisi Dupin 1968 ; 4, pl. 1 figs 7–12. Upper Jurassic, France.

Gonyaulacysta granulata (Klement) Sarjeant, comb. nov., =*Gonyaulax granulata* Klement, 1960; 39–41, pl. 4 figs. 10–13, text-figs. 18–20. Upper Jurassic, Germany.

Gonyaulacysta granuligera (Klement) Sarjeant, comb. nov., =*Gonyaulax granuligera* Klement, 1960 ; 41–2, pl. 5 figs. 4–5. Upper Jurassic, Germany.

Gonyaulacysta hadra Sarjeant, 1966b ; 119–21, pl. 14 fig. 1, text-fig. 28. Lower Cretaceous, England.

Gonyaulacysta helicoidea (Eisenack & Cookson) Sarjeant, 1966b ; 116–17, pl. 13 figs. 7–8, pl. 15 figs. 8–9, text-fig. 26, =*Gonyaulax helicoidea* Eisenack & Cookson, 1960 ; 2–3, pl. 2, figs. 4–9. Lower Cretaceous, Australia.

Gonyaulacysta hyaloderma (Deflandre, 1939 ; 144, pl. 6 figs 3–4) Sarjeant, 1967 ; 252. Upper Jurassic, France.

Gonyaulacysta hyalodermopsis (Cookson & Eisenack) Sarjeant, comb. nov., =*Gonyaulax hyalodermopsis* Cookson & Eisenack, 1958 ; 34, pl. 3 figs. 11–12, text-figs. 5–6. Lower Cretaceous, Australia.

Gonyaulacysta longicornis (Downie) Sarjeant, comb. nov., =*Gonyaulax longicornis* Downie, 1957 ; 420, pl. 20 fig. 8, text-figs. 2a–b. Upper Jurassic, England.

Gonyaulacysta kostromiensis (Vozzhennikova) Sarjeant, comb. nov., =*Gonyaulax kostromiensis* Vozzhennikova, 1967, 85–6, pl. 26, figs. 1–6, pl. 27, figs. 1–2. Lower Cretaceous, U.S.S.R.

?***Gonyaulacysta mamillifera*** (Deflandre) Sarjeant, comb. nov., =*Gonyaulax mamillifera* Deflandre, 1939 ; 143, pl. 6 fig. 1. Upper Jurassic, France.

Gonyaulacysta microceras (Eisenack) Clarke & Verdier, 1967 ; 31, =*Gonyaulax microceras* Eisenack, 1958 ; 391, pl. 21 figs. 12–13. Lower Cretaceous, Germany.

Gonyaulacysta monacantha (Deflandre, 1935 ; 228, pl. 6 fig. 1) Sarjeant, 1967 ; 252. Upper Cretaceous, France.

?***Gonyaulacysta nannotrix*** (Deflandre) Sarjeant, comb. nov., =*Gonyaulax nannotrix* Deflandre, 1939 ; 143, pl. 6 fig. 7. Upper Jurassic, France.

Gonyaulacysta nuciformis (Deflandre, 1938 ; 180, pl. 8 figs. 4–6, emend. Sarjeant, 1962b ; 482, pl. 6 fig. 6, text-fig. 4) Sarjeant, 1968 ; 227, pl. 3 fig. 4. Upper Jurassic, France. (Originally placed by Deflandre in the genus *Palaeoperidinium* : later transferred to *Gonyaulax* by Sarjeant, 1962b).

Gonyaulacysta obscura (Lejeune-Carpentier) Sarjeant, comb. nov., =*Gonyaulax obscura* Lejeune-Carpentier, 1946 ; 191–3, text-figs. 3–5. Upper Cretaceous, Belgium.

Gonyaulacysta pachyderma (Deflandre) Sarjeant, comb. nov., =*Gonyaulax pachyderma* Deflandre, 1938 ; 176–8, pl. 7 figs. 6–10, text-figs. 7–10. Upper Jurassic, France.

Gonyaulacysta palla Sarjeant, 1966b ; 113–4, pl. 13 figs. 3–4, text-fig. 24. Lower Cretaceous, England.

Gonyaulacysta parorthoceras Davey, 1968b ; 1 (=*G. orthoceras* Sarjeant, 1966b ; 121–3, pl. 14 figs. 5–6, text-fig. 29, =*Gonyaulax orthoceras* Eisenack, 1958, pl. 21 figs. 3–11, pl. 24 fig. 1, text-figs. 2–3, pars). Lower Cretaceous, England.

Gonyaulacysta perforans (Cookson and Eisenack) Sarjeant, comb. nov., =*Gonyaulax perforans* Cookson & Eisenack, 1958 ; 30–32, pl. 2 figs. 1–4, 7, 8, text-figs. 8–9. Upper Jurassic, Papua.

Gonyaulacysta pyra (Drugg) Sarjeant, comb. nov., =*Gonyaulax pyra* Drugg, 1967 ; 14, pl. 1 fig. 17, pl. 9 figs. 6a–b. Upper Cretaceous-Paleocene, California, U.S.A.

Gonyaulacysta sarjeanti (Vozzhennikova) Sarjeant, comb. nov., =*Gonyaulax sarjeanti* Vozzhennikova, 1967 ; 87–8, pl. 31, figs. 1–3. Upper Jurassic, U.S.S.R.

Gonyaulacysta scarburghensis Sarjeant, 1964 ; 472–3 (=*Gonyaulax areolata* Sarjeant, 1961a ; 95–7, pl. 13 fig. 13, text-fig. 5, nom. nud.). Upper Jurassic, England.

Gonyaulacysta scotti (Cookson & Eisenack) Sarjeant, comb. nov., =*Gonyaulax scotti* Cookson & Eisenack, 1958 ; 30, pl. 2 figs. 5–6. Upper Jurassic, Australia.

Gonyaulacysta serrata (Cookson & Eisenack) Sarjeant, comb. nov., =*Gonyaulax serrata* Cookson & Eisenack, 1958 ; 34, pl. 3 fig. 2, text-figs. 12–14. Upper Jurassic–Lower Cretaceous, Papua.

?*Gonyaulacysta tenuiceras* (Eisenack) Sarjeant, comb. nov., =*Gonyaulax tenuiceras* Eisenack, 1958 ; 389–91, pl. 21 figs. 14–15, pl. 22 figs. 1–3, pl. 24 fig. 2, text-figs. 4–5. Lower Cretaceous, Germany.

Gonyaulacysta tenuicornuta (Cookson & Eisenack) Sarjeant, comb. nov., =?*Leptodinium tenuicornutum* Cookson & Eisenack, 1962 ; 478, pl. 3 figs. 12–13, text-fig. 1a, b. ?Lower Cretaceous, Australia.

Gonyaulacysta tenuitabulata (Gerlach) Sarjeant, comb. nov., =*Gonyaulax tenuitabulata* Gerlach, 1961 ; 159–61, pl. 25 figs. 10–11, text-figs. 1–3. Oligocene-Miocene, Germany.

?*Gonyaulacysta transparens* (Sarjeant) Sarjeant, comb. nov., =*Gonyaulax transparens* Sarjeant, 1959 ; 334–5, pl. 13 fig. 3, text-fig. 3. Middle Jurassic England.

Gonyaulacysta wetzeli (Lejeune-Carpentier) Sarjeant, comb. nov., =*Gonyaulax wetzeli* Lejeune-Carpentier, 1939 ; 525–9, text-figs. 1–2. Upper Cretaceous, Germany.

Gonyaulacysta whitei Sarjeant, 1966b ; 126–8, pl. 14 fig. 2, text-fig. 32. Upper Cretaceous, England.

Genus ***LEPTODINIUM*** Klement 1960 emend. Wall 1967, emend.

1960 *Leptodinium* gen. nov. Klement : 45.
1965 *Leptodinium* Klement ; Norris & Sarjeant : 37.
1966 *Leptodinium* Klement ; Loeblich & Loeblich : 38.
1966b *Leptodinium* Klement ; emend. Sarjeant : 133–4.
1967 *Leptodinium* Klement ; emend. Wall : 104.

EMENDED DIAGNOSIS. Proximate dinoflagellate cysts, spheroidal, ovoidal, ellipsoidal or polyhedral, with reflected tabulation 3–4′, 0–1a, 6″, 6c, 5–6‴, 1p, 0–1 p.v., 1⁗, 0–x s. Apical, median and antapical horns lacking. Cingulum strongly or weakly helicoid, laevorotatory ; cingular plates well or poorly marked. Sulcus generally but not constantly extending onto epitract, undivided or subdivided into

a variable number of small plates. Rarely, an apical or an antapical pericoel may be present (but not both) ; the two shell layers are otherwise in continuous contact. Sutures typically marked by ridges or low crests (perforate or imperforate), without spines or denticles. Height of crests always less (and typically markedly less) than $\frac{1}{4}$ of shell width. A precingular single-plate archaeopyle, formed by loss of plate 3″, is developed, the operculum typically becoming wholly detached ; in some specimens, the archaeopyle may not be developed. Surface of periphragm smooth, granular, or punctate. Forms with nodose or reticulate surface have not been encountered and forms with crest spines or with general spine cover are excluded.

TYPE SPECIES. ***Leptodinium subtile*** Klement, 1960 ; 46–47, pl. 6 figs. 1–4, text-figs. 23–24. Upper Jurassic (Kimmeridgian), Germany.

REMARKS. The diagnosis here formulated is an expansion of that given by Wall (1967) : it differs in being more detailed and in permitting the inclusion of forms showing differentiation of the ventral surface into plates. Species with an apical horn are allocated to *Gonyaulacysta* ; species with sutures marked by lines of high spines are placed in *Hystrichogonyaulax* gen. nov.; species with a general spine cover are placed in the genus *Acanthaulax*. The currently known range of the genus *Leptodinium*, as here defined, is Upper Jurassic to Recent.

OTHER SPECIES.

Leptodinium aceras (Eisenack) Sarjeant, comb. nov., =*Gonyaulax aceras* Eisenack, 1958 ; 391–2, pl. 21 figs. 1–2. Lower Cretaceous, Germany.

Leptodinium aculeatum Wall, 1967 ; 104–5, pl. 14 figs. 18–19, text-figs. 3C, 3D. Pleistocene—Recent, Yucatan Basin, Caribbean Sea.

Leptodinium alectrolophum Sarjeant, 1966b ; 134–5, pl. 15 figs. 3–6, text-fig. 34. Lower Cretaceous, England.

Leptodinium amabilis (Deflandre) Sarjeant, comb. nov., =*Gonyaulax amabilis* Deflandre, 1939 ; 143, pl. 6 fig. 8. Upper Jurassic, France.

Leptodinium arcuatum Klement, 1960 ; 48, pl. 6 figs 5–6. Upper Jurassic, Germany.

Leptodinium clathratum (Cookson & Eisenack) Sarjeant, comb. nov., =*Gonyaulax clathrata* Cookson & Eisenack, 1960b ; 246–7, pl. 37 fig. 5, text-fig. 2. Upper Jurassic, Australia.

?*Leptodinium crassinervum* (Deflandre) Sarjeant, comb. nov., =*Palaeoperidinium crassinervum* Deflandre, 1939 ; 144, pl. 6 fig. 5. (Transfer of this species to *Gonyaulacysta* was proposed by Sarjeant, 1967 ; 248–9). Upper Jurassic, France.

Leptodinium delicatum (Davey) Sarjeant, comb. nov., =*Gonyaulacysta delicata* Davey, 1968a ; 123–4, pl. 1, figs. 7, 8, text-figs. 10A,B. Upper Cretaceous, Saskatchewan, Canada.

Leptodinium eumorphum (Cookson & Eisenack, 1960b ; 246, pl. 37 figs. 1–3, text-fig. 3) Eisenack, 1961 ; 324. Upper Jurassic, Australia.

Leptodinium freakei (Sarjeant) Sarjeant, comb. nov., =*Gonyaulax freakei* Sarjeant, 1963b ; 85–6, pl. 1 figs. 1–3. Upper Jurassic, England.

Leptodinium maculatum Cookson & Eisenack, 1961 ; 40, pl. 2 figs. 5–6. ?Upper Eocene, Rottnest Island, Australia.

Leptodinium margaritiferum (Cookson & Eisenack) Sarjeant, comb. nov., =*Gonyaulax margaritifera* Cookson & Eisenack, 1960a ; 5–6, pl. 2 figs. 1–2, text-fig. 1. Upper Cretaceous, Western Australia.

Leptodinium membranigerum Gerlach, 1961 ; 162–165, pl. 26 figs. 1–4, 7, text-figs 4,5. Oligocene-Miocene, Germany.

Leptodinium millioudi (Sarjeant) Sarjeant, comb. nov., =*Gonyaulax millioudi* Sarjeant, 1963b ; 86–88, pl. 1 figs. 4–7. Upper Jurassic, Switzerland.

Leptodinium mirabile Klement, 1960 ; 48–50, pl. 6 figs. 7–10, text-fig. 25–7. Upper Jurassic, Germany.

?*Leptodinium mosaicum* (Downie) Sarjeant, comb. nov., =*Palaeoperidinium mosaicum* Downie, 1957 ; 424, pl. 20 fig. 7, text-fig. 2f. (Transfer of this species to *Gonyaulacysta* was proposed, as a provisional measure, by Sarjeant 1967 ; 253). Upper Jurassic, England.

Leptodinium paradoxum Wall, 1967 ; 106–7, pl. 15 figs. 5–8, text-figs. 2, 3A, 3B. Miocene—Recent, Yucatan Basin, Caribbean Sea.

?*Leptodinium pilum* (Gocht) Sarjeant, comb. nov., =*Palaeoperidinium pilum* Gocht, 1959 ; 56–7, pl. 6 fig. 14, pl. 8 fig. 8. (Transfer of this species to *Gonyaulacysta* was proposed, as a provisional measure, by Sarjeant, 1967 ; 255). Lower Cretaceous, Germany.

Leptodinium porosum (Lejeune-Carpentier) Sarjeant, comb. nov., =*Gonyaulax porosa* Lejeune-Carpentier, 1946 ; 193. 196, text-fig. 6. Upper Cretaceous, Belgium.

Leptodinium sphaericum Wall, 1967 ; 108, pl. 15 figs. 11–15, text-fig. 2a–c. Pleistocene—Recent, Yucatan Basin, Caribbean Sea.

Leptodinium strialatum Wall, 1967 ; 107–8, pl. 15 figs. 9–10, text-fig. 5. Miocene—Recent, Yucatan Basin, Caribbean Sea.

Leptodinium striatum (Clarke & Verdier) Sarjeant, comb. nov., =*Gonyaulacysta striata* Clarke and Verdier, 1967 ; 31–32, pl. 4 figs. 11–13, pl. 5 fig. 15, text-fig. 12. Upper Cretaceous, England.

Genus ***HYSTRICHOGONYAULAX*** gen. nov.

Derivation of name. In reference to the *Gonyaulax*-type tabulation exhibited. and to the presence of spines on the sutures.

Diagnosis. Proximate dinoflagellate cysts, spheroidal, ovoidal, ellipsoidal or polyhedral, with the reflected tabulation 3–4′, 0–1a, 6″, 6c, 5–6‴, 1p, 0–1 p.v., 1⁗, 0–x s. Apical, median and antapical horns lacking. Cingulum strongly or weakly helicoid, laevorotatory ; cingular plates well or poorly marked. Sulcus generally but not constantly extending onto the epitract, undivided or subdivided into a variable number of small plates. Rarely, an apical or an antapical pericoel may be present (but not both) ; the two shell layers are otherwise in continuous contact. Sutures marked by lines or low ridges from which arise isolated spines ; the length of spines may vary according to position on the test (e.g. the spines

ringing the antapex may be longer than the others), or may be relatively constant. The spines may be simple or may bifurcate or ramify near the tips : their length is constantly less than $\frac{1}{4}$ of the longest shell cross-measurement. A precingular single-plate archaeopyle, formed by loss of plate 3″, is developed. Surface of periphragm smooth, granular or punctate. Forms with a nodose or reticulate surface have not, to date, been encountered : those with a general spine cover are excluded.

TYPE SPECIES. ***Hystrichogonyaulax cornigera*** (Valensi) Sarjeant, comb. nov., =*Gonyaulax cornigerum* (sic) Valensi, 1953 ; 27, pl. 1 figs. 4, 8, 10, pl. 2 figs. 1–2, pl. 13 fig. 5, text-fig. 2a. Middle Jurassic (Upper Bathonian), France.

OTHER SPECIES. ***Hystrichogonyaulax nealei*** (Sarjeant) Sarjeant, comb. nov., =*Gonyaulax nealei* Sarjeant, 1962 ; 480–1, pl. 69 fig. 1, text-fig. 2. Upper Jurassic, England.

REMARKS. This new genus corresponds to *Leptodinium* in its general morphology, differing in the possession of long sutural spines instead of low crests. It is most abundant in the Middle Jurassic and is characteristically numerous in Northwest European Bathonian sediments : the total known range is Middle to lower Upper Jurassic. On morphological grounds, it might be visualized as possibly ancestral to the genus *Gonyaulacysta* (which includes the species *G. cladophora*, with similar sutural spines but with an apical horn) and to the genus *Leptodinium*, by loss of the sutural spines ; at present, however, this must be regarded as a speculation only.

Other generic reallocations

Dichadogonyaulax pannea (Norris) Sarjeant, comb. nov., =*Leptodinium panneum* Norris, 1965 ; 796–8, figs. 3, 10–13. Upper Jurassic, England.

Dichadogonyaulax schizoblata (Norris) Sarjeant, comb. nov., =*Leptodinium schizoblatum* Norris, 1965 ; 798–800, figs. 4–5, 14–17. Upper Jurassic, England.

?*Litosphaeridium striatoconus* (Deflandre & Cookson) Sarjeant, comb. nov., =*Hystrichosphaeridium striatoconus* Deflandre & Cookson, 1955 ; 275–6, pl. 2, fig. 10, text-fig. 36 (Transferred to *Baltisphaeridium* by Downie & Sarjeant 1963 ; 92). Upper Cretaceous, Australia.

Meiourogonyaulax bulloidea (Cookson & Eisenack) Sarjeant, comb. nov., =*Gonyaulax bulloidea* Cookson & Eisenack, 1960b ; 247, pl. 37 fig. 11 text-fig. 4. Upper Jurassic, Western Australia.

Meiourogonyaulax caytonensis (Sarjeant) Sarjeant, comb. nov., =*Gonyaulax caytonensis* Sarjeant, 1959 ; 330–2, pl. 13 fig. 1, text-fig. 1. Middle Jurassic, England.

?*Meiourogonyaulax cristulata* (Sarjeant) Sarjeant, comb. nov., =*Gonyaulax cristulata* Sarjeant, 1959 ; 332–4, pl. 13 fig. 2, text-fig. 2. Middle Jurassic, England.

Meiourogonyaulax decapitata (W. Wetzel) Sarjeant, comb. nov., =*Gonyaulax decapitata* W. Wetzel, 1966 ; 869, pl. 16 figs 7a–b. Middle Jurassic, Germany.

Meiourogonyaulax superornata (W. Wetzel) Sarjeant, comb. nov., =*Gonyaulax superornata* W. Wetzel, 1966 ; 869–870, pl. 16 figs 8a–b. Middle Jurassic, Germany.

Polysphaeridium belgicum Sarjeant, sp. nov., =*Hystrichosphaeridium fluctuans* sensu Pastiels, 1948 ; 40, pl. 3 fig. 16, *non* Eisenack, 1938 ; 230–1, pl. 16 fig. 1 (Pastiels wrongly cites this as Eisenack 1937). Holotype : the specimen figured by Pastiels, 1948 ; pl. 3 fig. 16. Dimensions : shell $30 \times 35\mu$, appendages 12 μ long, overall span 60 μ. Eocene—Artesian well, Gand, Belgium.

Psaligonyaulax apatela (Cookson & Eisenack) Sarjeant, comb. nov., =*Scriniodinium apatelum* Cookson & Eisenack, 1960b ; 249, pl. 37 figs. 12–13. Upper Jurassic, Australia.

Psaligonyaulax simplicia (Cookson & Eisenack) Sarjeant, comb. nov., =*Rottnestia simplicia* Cookson & Eisenack, 1961 ; 42, 44, pl. 2 figs. 3–4, text-figs. 1 e–f. Eocene, Rottnest Island, Australia.

Rhaetogonyaulax chaloneri (Sarjeant), comb. nov., =*Gonyaulax chaloneri* Sarjeant, 1963a ; 354, text-figs. 2 (right), 3. Upper Triassic, England.

IV. GENERIC REALLOCATIONS PROPOSED JOINTLY BY R. J. DAVEY C. DOWNIE W. A. S. SARJEANT & G. L. WILLIAMS

Areoligera galea (Maier) Davey, Downie, Sarjeant & Williams, comb. nov., =*Galea galea* Maier, 1959 ; 306, pl. 29 fig. 4. (Transferred to *Baltisphaeridium* by Sarjeant, 1964 ; 176). Oligocene, Germany.

Areoligera lychnea (Maier) Davey, Downie, Sarjeant & Williams, comb. nov., =*Galea lychnea* Maier, 1959 ; 310, pl. 30 fig. 6. (Transferred to *Baltisphaeridium* by Sarjeant, 1964 ; 176). Miocene, Germany.

Areoligera twistringensis (Maier) Davey, Downie, Sarjeant & Williams, comb. nov., =*Galea twistringensis* Maier, 1959 ; 308–9, pl. 30 figs. 3–4. (Transferred to *Baltisphaeridium* by Sarjeant, 1964 ; 176). Oligocene, Germany.

Cleistosphaeridium ashdodense (Rossignol) Davey, Downie, Sarjeant and Williams, comb. nov., =*Hystrichosphaeridium ashdodense* Rossignol, 1962 ; 132, pl. 2 fig. 2. (Transferred to *Baltisphaeridium* by Downie & Sarjeant, 1964; 87. According to Wall 1967 ; 109, this species is a synonym of *Lingulodinium machaerophorum*). Quaternary, Israel.

?Cleistosphaeridium danicum (W. Wetzel) Davey, Downie, Sarjeant & Williams, comb. nov., =*Areoligera danica* W. Wetzel, 1952 ; 396–7, pl. A fig. 5, text-fig. 8. (Transferred to *Hystrichosphaeridium* by W. Wetzel, 1955 ; 34 ; transferred to *Baltisphaeridium* by Downie and Sarjeant, 1963 ; 91). Paleocene, Denmark.

Cleistosphaeridium echinoides (Maier) Davey, Downie, Sarjeant & Williams, comb. nov., =*Hystrichosphaeridium echinoides* Maier, 1959 ; 318–19, pl. 32 figs. 5–6. (Transferred to *Baltisphaeridium* by Downie & Sarjeant, 1963 ; 91). Oligocene, Germany.

Cleistosphaeridium ehrenbergi (Deflandre) Davey, Downie, Sarjeant & Williams, comb. nov., =*Hystrichosphaeridium ehrenbergi* Deflandre, 1947 ; text-fig. 1 no. 5. (Transferred to *Baltisphaeridium* by Sarjeant, 1961 ; 103). Middle Jurassic, France.

Cleistosphaeridium leve (Maier) Davey, Downie, Sarjeant & Williams, comb. nov., =*Galea levis* Maier, 1959 ; 308, pl. 30 figs. 1–2 (Transferred to *Baltisphaeridium* by Sarjeant, 1964 ; 176). Oligocene–Miocene, Germany.

Cleistosphaeridium lumectum (Sarjeant) Davey, Downie, Sarjeant & Williams, comb. nov., =*Baltisphaeridium lumectum* Sarjeant, 1960 ; 139–40, pl. 6, fig. 1, text-fig. 2. Upper Jurassic, England.

Cleistosphaeridium multifurcatum (Deflandre) Davey, Downie, Sarjeant & Williams, comb. nov., =*Hystrichosphaeridium multifurcatum* Deflandre, 1937 ; 76, pl. 16 figs. 1–3 (Transferred to *Baltisphaeridium* by Klement, 1960 ; 59). Upper Cretaceous, France.

?Cleistosphaeridium oligacanthum (W. Wetzel) Davey, Downie, Sarjeant & Williams, comb. nov., =*Hystrichosphaeridium oligacanthum* W. Wetzel, 1952 ; 402–3, pl. A fig. 8, text-figs. 21–2 (Transferred to *Baltisphaeridium* by Downie & Sarjeant, 1963 ; 91). Paleocene, Baltic Region.

Cleistosphaeridium pectiniforme (Gerlach) Davey, Downie, Sarjeant & Williams, comb. nov., =*Baltisphaeridium pectiniforme* Gerlach, 1961 ; 195, pl. 28 fig. 14, text-fig. 18. Oligocene, Germany.

Cleistosphaeridium polytrichum (Valensi) Davey, Downie, Sarjeant & Williams, comb. nov., =*Hystrichosphaeridium polytrichum* Valensi, 1947 ; 818, text-fig. 4 (Transferred to *Baltisphaeridium* by Sarjeant, 1959 ; 339). Middle Jurassic, France.

?Cleistosphaeridium spiralisetum (de Wit) Davey, Downie, Sarjeant & Williams, comb. nov., =*Hystrichosphaeridium spiralisetum* de Wit, 1943 ; 383, text-figs. 2, 11 (Transferred to *Baltisphaeridium* by Downie & Sarjeant, 1964 ; 97). Upper Cretaceous, Netherlands.

Cleistosphaeridium tiara (Klumpp) Davey, Downie, Sarjeant & Williams, comb. nov., =*Hystrichosphaeridium tiara* Klumpp, 1953 ; 390–1, pl. 17 figs. 8–10 (Ttransferred to *Baltisphaeridium* by Downie & Sarjeant, 1963 ; 92). Eocene Germany.

Cleistosphaeridium tribuliferum (Sarjeant) Davey, Downie, Sarjeant & Williams, comb. nov., =*Baltisphaeridium tribuliferum* Sarjeant, 1962 ; 487–8, pl. 70 fig. 4, text-figs. 6c, 7. Upper Jurassic, England.

Exochosphaeridium palmatum (Deflandre & Courteville) Davey, Downie, Sarjeant & Williams, comb. nov., =*Hystrichosphaeridium palmatum* Deflandre & Courteville, 1939 ; 101–2, pl. 3 fig. 1 (Transferred to *Baltisphaeridium* by Downie & Sarjeant, 1963 ; 91). Upper Cretaceous, France.

?Exochosphaeridium pseudhystrichodinium (Deflandre) Davey, Downie, Sarjeant & Williams, comb. nov., =*Hystrichosphaeridium pseudhystrichodinium*

Deflandre, 1937 ; 73, pl. 15 figs. 3–4 (Transferred to *Baltisphaeridium* by Downie & Sarjeant, 1963 ; 93). Upper Cretaceous, France.

Prolixosphaeridium mixtispinosum (Klement) Davey, Downie, Sarjeant & Williams, comb. nov., =*Baltisphaeridium mixtispinosum* Klement, 1960 ; 58–9, pl. 6 figs. 17–19. Upper Jurassic, Germany.

Prolixosphaeridium parvispinum (Deflandre) Davey, Downie, Sarjeant & Williams, comb. nov., =*Hystrichosphaeridium xanthiopyxides* var. *parvispinum* Deflandre, 1937 ; 29, pl. 16 fig. 5 (Raised to specific rank, as *Hystrichosphaeridium parvispinum*, by Cookson & Eisenack, 1958 ; 45 ; transferred to *Baltisphaeridium* by Klement, 1960 ; 59). Upper Cretaceous, France.

?*Prolixosphaeridium xanthiopyxides* (O. Wetzel) Davey, Downie, Sarjeant & Williams, comb. nov., =*Hystrichosphaera xanthiopyxides* O. Wetzel, 1933, 44–5 ; pl. 4 fig. 25 (Transferred to *Hystrichosphaeridium* by Deflandre, 1937 ; 77 ; transferred to *Baltisphaeridium* by Klement, 1960 ; 59). Upper Cretaceous, Germany.

Systematophora placacantha (Deflandre & Cookson) Davey, Downie, Sarjeant & Williams, comb. nov., =*Hystrichosphaeridium placacanthum* Deflandre & Cookson, 1955 ; 276–7, pl. 9 figs. 1–3 (Transferred to *Baltisphaeridium* by Downie & Sarjeant, 1963 ; 92). Miocene, Australia.

V. GENERIC REALLOCATIONS PROPOSED BY G. L. WILLIAMS & C. DOWNIE

Adnatosphaeridium aemulum (Deflandre) Williams & Downie, comb. nov., =*Hystrichosphaeridium aemulum* Deflandre, 1938 ; 187–9, pl. 9 fig. 12, pl. 10 figs. 5–8, pl. 11 figs. 1–7 (Transferred to *Cannosphaeropsis* by Deflandre, 1947a ; 1574). Upper Jurassic, France.

Adnatosphaeridium caulleryi (Deflandre) Williams & Downie, comb. nov., =*Hystrichosphaeridium caulleryi* Deflandre, 1938 ; 189, pl. 11 figs. 2–3 (Transferred to *Cannosphaeropsis* by Deflandre, 1947 ; 1574). Upper Jurassic, France.

Adnatosphaeridium filamentosum (Cookson & Eisenack) Williams & Downie, comb. nov., =*Cannosphaeropsis filamentosa* Cookson & Eisenack, 1958 ; 47–8, pl. 7 figs. 8–9, pl. 8 figs. 1–2. Middle–Upper Jurassic, Australia.

Adnatosphaeridium filiferum (Cookson & Eisenack) Williams & Downie, comb. nov., =*Cannosphaeropsis utinensis* var. *filifera* Cookson & Eisenack, 1958 ; 46, pl. 7 fig. 4 (Raised to specific rank, as *Cannosphaeropsis filifera*, by Cookson & Eisenack, 1960a ; 8–9). Upper Cretaceous, Australia.

Hystrichokolpoma clavigera (Deflandre) Williams & Downie, comb. nov., =*Hystrichosphaeridium clavigerum* Deflandre, 1937 ; 71, pl. 14 figs. 1–2 (Transferred to *Baltisphaeridium* by Downie & Sarjeant, 1963 ; 91). Upper Cretaceous, France.

VI. TAXONOMIC REVISIONS MADE BY OTHER AUTHORS

Taxonomic revisions made by other authors in the period since publication of our 'Studies on Mesozoic and Cainozoic dinoflagellate cysts' have caused the omission, from the preceding sections, of a number of species transferred to new genera in the earlier work without new combinations for them being validly published. It is felt that these should be briefly listed here, in order to provide comprehensive coverage.

(a) The species *Hystrichosphaeridium zoharyi* Rossignol, 1962, whose transfer to the genus *Polysphaeridium* was tentatively proposed by Davey & Williams (1966b ; 95), has been made type for a new genus, *Hemicystodinium*, by Wall, (1967 ; 110) on the basis of its development of an epitractal archaeopyle.

(b) The species *Hystrichosphaeridium israelianum* Rossignol, 1962 (placed in the genus *Baltisphaeridium* by Downie and Sarjeant, 1964) and *Hystrichosphaeridium centrocarpum* Deflandre and Cookson, 1955 (placed in the genus *Baltisphaeridium* by Gerlach, 1961), were transferred to the genus *Cleistosphaeridium* by Davey, Downie, Sarjeant & Williams (1966 ; 170). Both have been placed in a new genus, *Operculodinium*, by Wall (1967 ; 110–11), *H. centrocarpum* being chosen as type. This genus resembles *Exochosphaeridium* Davey, Downie, Sarjeant & Williams (1966 ; 165) in its development of a single-plate precingular archaeopyle, differing in the apparent absence of an enlarged apical process, and in the presence of striations on the bases of the processes.

(c) The species *Hystrichosphaeridium machaerophorum* Deflandre & Cookson, 1955 (placed in the genus *Baltisphaeridium* by Downie & Sarjeant, 1963), was transferred to the genus *Cleistosphaeridium* by Davey, Downie, Sarjeant & Williams (1966 ; 165). It has been made the type of a new genus, *Lingulodinium*, by Wall (1967 ; 109–10), on the basis of its possession of a precingular archaeopyle formed by loss of the equivalents of four or five plate areas.

(d) In three instances, the proposed type species of new genera formulated in our earlier work were not initially validly transferred to those genera (I.C.B.N. Art. 33) and were subsequently validly transferred by Loeblich & Loeblich, (1968). These are : *Dichadogonyaulax culmula* (Norris, 1965) Leoblich & Loeblich, 1968 ; 211 [=*Dichadogonyaulax culmula* (Norris, 1965) Sarjeant, 1966b ; 153, nom. nud.] ; *Duosphaeridium nudum* (Cookson, 1965) Loeblich & Loeblich, 1968 ; 211 [=*Duosphaeridium nudum* (Cookson, 1965) Davey & Williams, 1966b ; 97, nom. nud.] ; and *Rhaetogonyaulax rhaetica* (Sarjeant, 1963) Loeblich & Loeblich, 1968 ; 212 [=*Rhaetogonyaulax rhaetica* (Sarjeant, 1963), 1966 ; 97, nom. nud.].

(e) As a result of a redefinition of the genus *Cribroperidinium* Neale & Sarjeant (1962), proposed by Davey (1968a ; 125), the species *Gonyaulax edwardsi* Cookson & Eisenack 1958, *Gonyaulax muderongensis* Cookson & Eisenack 1958, and *Gonyaulax orthoceras* Eisenack 1958 *sensu stricto* (i.e. excluding *G. parorthoceras* Davey 1968b), whose reallocation to *Gonyaulacysta* was proposed by Sarjeant (1966 ; 130 ; 131 ; 121–3), are now transferred to *Cribroperidinium* (Davey 1968a ; 128).

Davey (*op. cit.*) also validly published the following combinations : *Cleistosphaeridium multifurcatum* (Deflandre, 1937), *Cleistosphaeridium polypes* (Cookson & Eisenack, 1962), *Cleistosphaeridium pseudhystrichodinium* (Deflandre, 1937) [wrongly spelled *pseudohystrichodinium* in all citations], *Hystrichokolpoma ferox* (Deflandre, 1937) emend., *Oligosphaeridium anthophorum* (Cookson & Eisenack, 1958) and *Oligosphaeridium reniforme* (Tasch, *in* Tasch, McClure & Oftedahl, 1964). He considered no change in the generic allocation of *Hystrichosphaeridium difficile* Manum & Cookson, 1964, to be necessary.

(f) Two recent large papers exhibit a high degree of taxonomic overlap with our 1966 volume. One of these (Morgenroth, 1966) has priority of publication by one month ; it is hoped that the systematic problems created will be sorted out in a later paper. The second (Clarke & Verdier, 1967) does not have priority : a short note, giving the resulting synonymy, has recently been published (Clarke, Davey, Sarjeant & Verdier, 1968).

(g) Pending a restudy of its holotype, no proposal of generic transfer is here made respecting *Hystrichosphaeridium tridactylites* Valensi, 1955a.

(h) A new name, *Acanthaulax*, was proposed to replace the invalid junior hononym *Acanthogonyaulax* by Sarjeant, 1968, and all constituent species were transferred.

VII. ERRATA AND CURATORIAL AMENDMENTS

The following errata have been noted and merit correction :

p. 28 line 20. For ' *nomen nudum* ', read ' *nomen oblitum* '.
p. 63 line 8. Revise to read ' V. 51708 (1) '.
p. 65 line 5. Revise to read ' Pl. 7 fig. 9 ; pl. 8 fig. 6 '
p. 70 Delete parentheses from : ' Maier 1959 ' (lines 15 and 24) ; 'Eisenack and Cookson, 1960 ' (line 18) ; ' Deunff, 1961 ' (line 20) ; and ' Mackó, 1957 ' (line 22).
p. 75 line 1. Revise to read ' V. 51709 (3) '.
line 6. Revise to read ' V. 51709 (1) '.
p. 78 Delete last sentence of ' Remarks '.
p. 80 Text-fig. 16. 1p and 1''' should be interchanged in both drawings.
p. 92 line 4. Alter to read ' *Polysphaeridium subtile* sp. nov.'
p. 95 line 12. Alter to read ' (Weiler, 1956) '.
p. 100 line 33. Alter to read ' *Homotryblium tenuispinosum* sp. nov.'
p. 133 lines 15–16. Insert between these lines ' Plate 22 fig. 2.'
line 22. Alter to read ' *heslertonensis*'.
p. 140 line 20. For ' junior homonym ' read ' junior synonym '.
p. 144 line 13. Revise to read ' V. 51710 (1) '.
p. 147 line 13. Alter to read ' *Xiphophoridium alatum* sp. nov.'
line 15. Correct page number to ' 487 '.
p. 154 line 20. Alter to read ' *Wanaea spectabilis* (Deflandre & Cookson), Cookson & Eisenack, 1958 '.

p. 166 line 26. Alter to read '*Cleistosphaeridium diversispinosum* sp. nov.'
p. 166 line 16. Alter to read '*Exochosphaeridium*'.
p. 167 line 5. Alter to read '*Cleistosphaeridium*'.
p. 170 line 21. Delete 'Miocene, Australia': insert 'Quaternary, Israel'.
pp. 182–198. Throughtout this section, the left and right antapical horns are interchanged in the descriptions. It is the *right* horn that is typically reduced or absent.
p. 195 lines 20, 21. Alter to read '*solida*'.
line 38. Alter to read '*solidum*'.
p. 197 line 28. Alter to read 'Sub-Genus WETZELIELLA (RHOMBODINIUM) (Gocht) Alberti, 1961'.
p. 201 line 29. Alter to read '*Paranetrelytron*'.
p. 219 line 10. Alter to read '*Membranilarnacia*'.
p. 225 line 3. Alter to read: '1948 *Membranilarnax pterospermoides* O. Wetzel, 1933, of Pastiels'.
p. 245 Index. Insert to give: '*Heslertonia heslertonensis* **133.** pl. 22 fig. 2'.

Caption for Plate 3. Explanations of Figures 3 and 4 should be transposed, and altered to read '*Cordosphaeridium*'.
Caption for Plate 9 fig. 6. Alter to read: '103·25 m'.
fig. 7. 'Holotype' should read: 'Paratype'. Figure shows left-to-right reversal.
Caption for Plate 10 fig. 4. Alter to read: 'V. 51708 (1)'.
Caption for Plate 11 fig. 9. Revise to read: '*disjunctum*'.
Caption for Plate 13 fig. 1. Alter to read: 'V. 51425 (2)'.
Caption for Plate 15 figs. 1–2. Correct to read: '*Gonyaulacysta*'.
fig. 5. Alter to read 'V. 51725 (1)'.

For curatorial reasons, it is proposed that slides containing a single specimen should not have a number 1 in parentheses. This proposal necessitates the following changes:

V. 51715 (1) becomes V. 51715 (p. 213, line 10).
V. 51720 (1) becomes V. 51720 (caption for Plate 23 fig. 6).
V. 51721 (1) becomes V. 51721 (p. 209 line 26: caption for Plate 22 fig. 5).
V. 51726 (1) becomes V. 51726 (p. 210 line 6; caption for Plate 21 fig. 4).
V. 51733 (1) becomes V. 51733 (p. 207 line 3; caption for Plate 21 fig. 1).
V. 51735 (1) becomes V. 51735 (p. 161 line 15; caption for Plate 9 fig. 6).
V. 51736 (1) becomes V. 51736 (p. 163 fig. 5; caption for Plate 9 fig. 8).

VIII. REFERENCES

Alberti, G. 1961. Zur Kenntnis mesozoischer und alttertiärer Dinoflagellaten und Hystrichosphaerideen von Nord—und Mitteldeutschland sowie einigen anderen europäischen Gebieten. *Palaeontographica*, Cassel, Stuttgart, **116A**: 1–58, pls. 1–12.

Brosius, M. 1963. Plankton aus dem nordhessischen Kasseler Meeressand (Oberoligozän). *Z. dt. geol. Ges.*, Berlin, **114**, 1: 32–56, pls. 1–8, text-figs. 1, 2, pls. 1, 2.

CLARKE, R. F. A., DAVEY, R. J., SARJEANT, W. A. S. & VERDIER, J.-P. 1968. A note on the nomenclature of some Upper Cretaceous and Eocene dinoflagellate taxa. *Taxon*, Utrecht, **17** : 181–3.

CLARKE, R. F. A. & VERDIER, J.-P. 1967. An investigation of microplankton assemblages from the Chalk of the Isle of Wight, England. *Verh. K. ned. Akad. Wet.*, Amsterdam, **24** (3), 1–96, pls. 1–17.

COOKSON, I. C. 1965. Cretaceous and Tertiary microplankton from south-eastern Australia. *Proc. R. Soc. Vict.*, Melbourne, n.s., **78** : 85–93, pls. 9–11.

COOKSON, I. C. & EISENACK, A. 1958. Microplankton from Australian and New Guinea Upper Mesozoic sediments. *Proc. R. Soc. Vict.*, Melbourne, **70**, 1 : 19–79, pls. 1–12.

——,—— 1960a. Microplankton from Australian Cretaceous sediments. *Micropaleontology*, New York, **6**, 1 : 1–18, pls. 1–3.

——, —— 1960b. Upper Mesozoic microplankton from Australia and New Guinea. *Palaeontology*, London, **2**, 2 : 243–61, pls. 37–39.

——, —— 1961. Tertiary microplankton from the Rottnest Island Bore, Western Australia. *J. Proc. R. Soc. W. Aust.*, Perth, **44** : 39–47, pls. 1–2, text-fig. 1.

——, —— 1962. Additional microplankton from Australian Cretaceous sediments. *Micropaleontology*, New York, **8**, 4 : 484–507, pls. 1–7.

DAVEY, R. J. 1968a. Non-Calcareous Microplankton from the Cenomanian of England, northern France and North America. Part 1. *Bull. Br. Mus. nat.*, London, **17**, 3, 105–180, pls. 1–11.

—— 1968b. *Gonyaulacysta parorthoceras*, a new species of dinoflagellate cyst. *Palaeont. afr.* Johannesburg, **17** : 1.

DAVEY, R. J., DOWNIE, C., SARJEANT, W. A. S. & WILLIAMS, G. L. 1966. Fossil dinoflagellate cysts attributed to *Baltisphaeridium*. *Bull. Br. Mus. nat. Hist. Geol.*, London, Suppl. **3** : 157–75, pls. 2–3 (pars), 9 (*pars*), 11 (*pars*).

DAVEY, R. J. & WILLIAMS, G. L. 1966a. The genera *Hystrichosphaera* and *Achomosphaera*. *Bull. Br. Mus. nat. Hist Geol.*, London, Supp. **3** : 28–52, pls. 1, 2–5 (pars), 9 (pars), tab. 2.

——, —— 1966b. The genus *Hystrichosphaeridium* and its allies. *Bull. Br. Mus. nat. Hist. Geol.*, London, Supp. **3** : 53–106, pls. 3–9 (*pars*), 10, 11 (*pars*), 12, tab. 3.

DEFLANDRE, G. 1935. Considérations biologiques sur les micro-organismes d'origine planctonique conservés dans les silex de la craie. *Bull. biol. Fr. Belg.*, Paris, **69** : 213–44, pls. 5–9.

—— 1937. Microfossiles des silex crétacés II. Flagellés incertae sedis. Hystrichosphaeridées. Sarcodinés. Organismes divers. *Annls. Paléont.*, Paris, **26** : 51–103, pls. 8–18.

—— 1938. Microplankton des mers jurassiques conservé dans les marnes de Villers-sur-Mer (Calvados). Étude liminaire et considérations générales. *Trav. Stn. Zool. Wimereux*, Paris, **13** : 147–200, pls. 5–11, text-figs. 1–10.

—— 1939. Sur les dinoflagellés des schistes bitumineux d'Orbagnoux (Jura). *Bull. Soc. fr. Microsc.*, Paris, **8**, 4 : 141–5, pl. 6.

—— 1946a. Hystrichosphaeridés II. Espèces du Secondaire et du Tertiaire. *Fichier micropaléont.* ser. 6. *Arch. Orig. Serv. Docum. C.N.R.S.*, no. **235**, parts I–V, cards 860–1019.

—— 1946b. Remarques sur la systématique des Hystrichosphères. *C.r. somm. Séanc. Soc. geol. Fr.*, Paris, **7** : 110–11.

—— 1947. Sur une nouvelle Hystrichosphère des silex crétacés et sur les affinitiés du genre *Cannosphaeropsis* O. Wetzel. *C.r. hebd. Séanc. Acad. Sci.*, Paris, **224** : 1574–76, figs. 1–5.

—— 1964. Quelques observations sur la systématique et la nomenclature des dinoflagellés fossiles. *Multicop. E.P.H.E. et illustration C.N.R.S.*, Paris : 1–8.

DEFLANDRE, G. & COOKSON, I. C. 1955. Fossil microplankton from Australian late Mesozoic and Tertiary sediments. *Aust. J. mar. Freshwat. Res.*, Melbourne, **6**, 2 : 242–313, pls. 1–9.

DEFLANDRE, G. & COURTEVILLE, M. 1939. Note préliminaire sur les microfossiles des silex crétacés du Cambrésis. *Bull. Soc. fr. Microsc.*, Paris, **8** : 95–106, pls. 1–3.

DOWNIE, C. 1957. Microplankton from the Kimeridge Clay. *Q. Jl. geol. Soc. Lond.*, **112** : 413–34, pl. 20.

DOWNIE, C. & SARJEANT, W. A. S. 1963. On the interpretation of some Hystrichosphere genera. *Palaeontology*. London, **6**, 1 : 83–96.

——, —— 1964. Bibliography and index of fossil dinoflagellates and acritarchs. *Mem. geol. Soc. Am.*, New York, **94** : 180 pp.

DRUGG, W. S. 1967. Palynology of the Upper Moreno Formation (late Cretaceous-Paleocene), Escarpado Canyon, California. *Palaeontographica*, Stuttgart, ser. B., **120** : 1–71, pls. 1–9.

DUPIN, F. 1968. Deux nouvelles espèces de Dinoflagellés du Jurassique d'Aquitaine. *Cah. micropaléont.*, Paris, ser 1, **8** : 1–5, pl. 1.

EISENACK, A. 1938. Hystrichosphaerideen und verwandte Formen in baltischen Silur. *Z. Geschiebeforsch.*, **14** : 1–30, pls. 1–4, text-figs. 1–7.

—— 1954. Mikrofossilien aus Phosphoriten des samlandischen Unter-Oligozäns und über die Einheitlichkeit der Hystrichosphaerideen. *Palaeontographica*, Stuttgart, ser. A., **105** : 49–95, pls. 7–12.

—— 1958. Mikroplankton aus dem norddeutschen Apt nebst einigen Bemerkungen über fossile Dinoflagellaten. *Neues Jb. Geol. Paläont., Abh.*, Stuttgart, **106**, 3 : 383–422, pls. 21–7.

—— 1961. Einige Erörterungen über fossile Dinoflagellaten nebst Ubersicht über die zur Zeit bekannten Gattungen. *Neues Jb. Geol. Paläont., Abh.*, Stuttgart, **112**, 3 : 281–324, pls. 33–7.

EISENACK, A. & COOKSON, I. C. 1960. Microplankton from Australian Lower Cretaceous sediments. *Proc. R. Soc. Vict.*, Melbourne, **72**, 1 : 1–11, pls. 1–3.

EISENACK, A. & KLEMENT, K. W. 1964. *Katalog der fossilen Dinoflagellaten, Hystrichosphären und verwandten Mikrofossilien.* Stuttgart : E. Schweizerbart. 887 pp., 9 pls.

GERLACH, E. 1961. Mikrofossilien aus dem Oligozän und Miozän Nordwestdeutschlands, unter besonderer Berucksichtigung der Hystrichosphaerideen und Dinoflagellaten. *Neues Jb. Geol. Paläont., Abh.*, Stuttgart, **112**, 2 : 143–228, pls. 25–9, text-figs. 1–23.

GOCHT, H. 1959. Mikroplankton aus dem nordwestdeutschen Neokom II. *Paläont. Z.*, Berlin, **33**, 1–2 : 50–89, pls. 3–8.

KLEMENT, K. W. 1960. Dinoflagellaten und Hystrichosphaerideen aus dem Unteren und Mittleren Malm Sudwestdeutschlands. *Palaeontographica* Cassel, Stuttgart, A, **114** : 1–104, pls. 1–10.

KLUMPP, B. 1953. Beitrag zur Kenntnis der Mikrofossilien des Mittleren und Oberen Eozän. *Palaeontographica*, Cassel, Stuttgart, **103**, A : 377–406, pls. 16–20, text-figs. 1–5.

LEJEUNE-CARPENTIER, M. 1939. L'étude microscopique des silex (7 ième Note). Un nouveau Péridinien crétacique, *Gonyaulax wetzeli*. *Annls. Soc. géol. Belg.*, Liège, **62**, 10–11 : B525–9., text-figs. 1, 2.

—— —— 1940. L'étude microscopique des silex (8 ième Note). Systématique et morphologie des " Tubifères ". *Annls. Soc. géol. Belg.*, Liège, **63**, 5 : B216–36, text-figs. 1–14.

—— —— 1941. L'étude microscopique des silex (9 ième Note). Sur *Hystrichosphaeridium hirsutum* (Ehrenberg) et quelques formes voisines. *Annls. Soc. géol. Belg.*, Liège, **63** (3) B, 71–92.

—— —— 1946. L'étude microscopique des silex (12 ième Note). Espèces nouvelles ou douteuses de *Gonyaulax*. *Annls. Soc. géol. Belg.*, Liège, **69**, 4 : B187–97, figs. 1–5.

LOEBLICH, A. R., Jnr. & LOEBLICH, A. R., III. 1966. Index to the genera, subgenera and sections of the Pyrrhophyta. *Stud. Trop. Oceanogr., Miami*, **3** : 94 pp.

——, —— 1968. Index to the genera, subgenera and sections of the Pyrrhophyta II. *J. Paleont.*, Tulsa, **42** : 210–13.

MAIER, D. 1959. Planktonunterschungen in tertiären und quatären marinen Sedimenten. *Neues Jb. Geol. Paläont., Abh.*, Stuttgart, **107**, 3 : 278–340, pls. 27–33.

MANUM, S. & COOKSON, I. C. 1964. Cretaceous microplankton in a sample from Graham Island, Arctic Canada, collected during the second " Fram " expedition (1898–1902), with notes on the microplankton from the Hassel Formation, Ellef Ringnes Island. *Skr. norske Vidensk-Akad.*, Oslo, n.s., **17** : 1–36, pls. 1–7.

MERRILL, J. A. 1895. Fossil sponges of the flint nodules in the Lower Cretaceous of Texas. *Bull. Mus. comp. Zool. Harv.*, Cambridge, Mass., **28**, 1 : 1–26, pl. 1.

MORGENROTH, P. 1967. Mikrofossilien und Konkretionen des Nordwestdeutschen Untereozäns. *Palaeontographica*, Stuttgart, ser. B, **119** : 1–53, pls. 1–11.

NEALE, J. W. & SARJEANT, W. A. S. 1962. Microplankton from the Speeton Clay of Yorkshire. *Geol. Mag.*, London, **99**, 5 : 439–58, pls. 19, 20.

NORRIS, G. 1965. Archeopyle structures in Upper Jurassic dinoflagellates from southern England. *N.Z. Jl. Geol. Geophys.*, Wellington, **8** : 792–806.

NORRIS, G. & SARJEANT, W. A. S. 1965. A descriptive index of genera of fossil Dinophyceae and Acritarcha. *Bull. geol. Surv. N.Z. Paleont.*, Wellington, **40**. 72 pp.

PASTIELS, A. 1948. Contributions à l'étude des microfossiles de l'Eocene belge. *Mém. Mus. r. Hist. nat. Belg.*, Bruxelles, **109** : 1–77, pls. 1–6.

PHILIPOTT, A. 1949. Contributions à la paléontologie des silex crétacés. Trois nouveaux microfossiles. *Bull. Soc. scient. Bretagne*, Rennes, **24** : 55–8, text-figs. 1–3.

POCOCK, S. A. J. 1962. Microfloral analysis and age determination of strata at the Jurassic-Cretaceous boundary in the Western Canada plains. *Palaeontographica*, Cassel, Stuttgart, **111**, B : 1–95, pls. 1–15.

READE, J. B. 1839. On some organic remains in the Flint of Chalk. *Ann. Mag. nat. Hist.*, London, **2** : 191–8, pls. 8–9.

ROSSIGNOL, M. 1962. Analyse pollinique de sédiments marins Quaternaires en Israël 11. Sediments Pleistocènes. *Pollen Spores*, Paris, **4**, 1 : 121–48, pls. 1, 2, tabs. 1, 2, map. 1.

SARJEANT. W. A. S. 1959. Microplankton from the Cornbrash of Yorkshire. *Geol. Mag.*, London, **96**, 5 : 329–46, pl. 13.

—— 1960. New Hystrichospheres from the Upper Jurassic of Dorset. *Geol. Mag.*, London **97**, 2 : 137–44, pl. 6, text-figs. 1–4.

—— 1961. Microplankton from the Kellaways Rocks and Oxford Clay of Yorkshire. *Palaeontology*, London, **4**, 1 : 90–118, pls. 13–15.

—— 1962. Microplankton from the Ampthill Clay of Melton, South Yorkshire. *Palaeontology*, London, **5**, 3 : 478–97, pls. 69–70.

—— 1963a. Fossil dinoflagellates from Upper Triassic sediments. *Nature, Lond.*, London, **199**, 4891 : 353–4, text-figs. 1–3.

—— 1963b. Two new Jurassic species of *Gonyaulax* (Dinophyceae). *Revue Micropaléont.*, Paris, **6**, 2 : 85–8, pl. 1.

—— 1964. Taxonomic notes on hystrichospheres and acritarchs. *J. Paleont.*, Tulsa, **38** : 173–7.

—— 1966a. The supposed "sponge spicules" of Merrill, 1895, from the Lower Cretaceous (Albian) of Texas. *Breviora*, Cambridge, Mass., **242**, 1–15, pl. 1, text-fig. A.

—— 1966b. Dinoflagellate cysts with *Gonyaulax*-type tabulation. *Bull. Br. Mus. nat. Hist. Geol.*, London, Supp. **3** : 107–56, pls. 13–16, tab. 4.

—— 1966c. Further dinoflagellate cysts from the Speeton Clay. *Bull. Br. Mus. nat. Hist. Geol.*, London, Supp. **3** : 199–214, pls. 21–3, tab. 5.

—— 1967. The genus *Palaeoperidinium* Deflandre (Dinophyceae). *Grana palynol.*, Stockholm, **7** : 243–58.

—— 1968. Microplankton from the Upper Callovian and Lower Oxfordian of Normandy. *Revue Micropaléont.*, Paris, **10** : 221–42, pls. 1–3.

TAPPAN, H. & LOEBLICH, A. R., Jnr. 1967. Review : Studies on Mesozoic and Cainozoic dinoflagellate cysts. *J. Paleont.*, Tulsa, **41** : 1030–33.

TASCH, P., MCCLURE, K. & OFTEDAHL, O. 1964. Biostratigraphy and taxonomy of a hystrichosphere-dinoflagellate assemblage from the Cretaceous of Kansas. *Micropaleontology*, New York, **10** : 189–206, pls. 1–3.

VALENSI, L. 1947. Note préliminaire à une étude des microfossiles des silex jurassiques de la région de Poitiers. *Cr. hebd. Séanc. Acad. Sci., Paris*, **225** : 816–8, figs. 1–8.

—— 1953. Microfossiles des silex du Jurassique moyen. Remarques pétrographiques. *Mém. Soc. géol. Fr.*, Paris, **68**, 100 pp., 7 figs.

VALENSI, L. 1955a. Sur quelques micro-organismes des silex crétacés du Magdalénien de Saint-Amand (Cher). *Bull. Soc. geol. Fr.*, **6**, 5 : 35–40, text-figs. 1–2.

—— 1955b. Étude micropaléontologique des silex du Magdalénien de Saint-Amand (Cher). *Bull. Soc. préhist. fr.*, Paris, **52**, 9–10 : 584–96, pls. 1–5.

VOZZHENNIKOVA, T. F. 1967. Iskopayemiye peridinei yurskikh, myelovikh : palaeogenovikh otlozheniy S.S.S.R. Moscow : Nauka : 1–347, pls. 1–120.

WALL, D. 1967. Fossil microplankton in deep-sea cores from the Caribbean Sea. *Palaeontology*, London, **10** : 95–123, pls. 14–16.

WETZEL, O. 1933. Die in organischer Substanz erhaltenen Mikrofossilien des Baltischen Kreide-Feuersteins. *Palaeontographica*, Cassel, Stuttgart, **77** : 141–88, figs. 1–10, **78** : 1–110, pls. 1–7.

WETZEL, W. 1952. Beitrag zur Kenntnis des dan-zeitlichen Meeresplanktons. *Geol. Jb.*, Berlin, (for 1950), **66** : 391–419, pl. A.

—— 1955. Die Dan-Scholle vom Katharinenhof (Fehmarn) und ihr Gehalt an Planktonen. *Neues Jb. Geol. Paläont., Mh.*, Stuttgart, **1** : 30–46, text-figs. 1–26, tab. 1.

—— 1966. Mikroorganismen aus jurassischen und Kretazischen Saurier-Gewölle. *Z. deutsch. geol. Ges.*, Berlin, Jg. 1964, **116** : 867–74, pls. 15–17.

WHITE, H. H. 1842. On fossil Xanthidia. *Microsc. J.*, London, **11** : 35–40, pl. 4.

WILLIAMS, G. L., & DOWNIE, C. 1966a. The genus *Hystrichokolpoma*. *Bull. Br. Mus. nat. Hist. Geol.*, London, Suppl. **3** : 176–81, pl. 17.

——, —— 1966b. *Wetzeliella* from the London Clay. *Bull. Br. Mus. nat. Hist. Geol.*, London, Supp. **3** : 182–98, pls. 18–20.

——, —— 1966c. Further dinoflagellate cysts from the London Clay. *Bull. Br. Mus. nat. Hist. Geol.*, London, Supp. **3** : 215–35, pls. 24–6.

WIT, R. DE. 1943. Hystrichosphaeridae in Limburgsche Vuursten. *Verh. ned. geol.-mijnb. Genoot.*'s Gravenhage, **13** : 363–92, text-figs. 1–15.

R. J. DAVEY, B.SC., PH.D., F.G.S.
Formerly of BERNARD PRICE INSTITUTE FOR PALAEONTOLOGICAL RESEARCH
UNIVERSITY OF THE WITWATERSRAND
JOHANNESBURG
SOUTH AFRICA

C. DOWNIE, B.SC., PH.D., F.G.S.
Dept. of Geology
UNIVERSITY OF SHEFFIELD
ENGLAND

W. A. S. SARJEANT, B.SC., PH.D., F.G.S., F.L.S.
Dept. of Geology
UNIVERSITY OF NOTTINGHAM
ENGLAND

G. L. WILLIAMS, B.SC., PH.D.
PAN-AMERICAN PETROLEUM CORP.
RESEARCH CENTER
TULSA
OKLAHOMA, U.S.A.

Printed in England by Staples Printers Limited at their Kettering, Northants, establishment

PERMIAN TO PALAEOCENE CALCAREOUS ALGAE (DASYCLADACEAE) OF THE MIDDLE EAST

G. F. ELLIOTT

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Supplement 4
LONDON: 1968

PERMIAN TO PALAEOCENE CALCAREOUS ALGAE (DASYCLADACEAE) OF THE MIDDLE EAST

BY

GRAHAM FRANCIS ELLIOTT

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Supplement 4
LONDON : 1968

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

In 1965 *a separate supplementary series of longer papers was instituted, numbered serially for each Department.*

This paper is Supplement 4 *of the Geological (Palaeontological) series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

World List abbreviation
Bull. Br. Mus. nat. Hist. (Geol.)

© Trustees of the British Museum (Natural History) 1968

TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)

Issued 8 *November*, 1968 *Price* £5 2*s*. 6*d*.

PERMIAN TO PALAEOCENE CALCAREOUS ALGAE (DASYCLADACEAE) OF THE MIDDLE EAST

By GRAHAM FRANCIS ELLIOTT

CONTENTS

SYNOPSIS

The fossil flora of calcareous chlorophyte algae, family Dasycladaceae, from the Permian to Palaeocene succession of the Middle East, is described and figured. This material has been selected principally from extensive rock collections made by geologists of the Iraq Petroleum Group in Iraq, Qatar, Oman and Hadhramaut. Advantage has also been taken of much fossil comparative material from the remainder of the Middle East, the European and African circum-Mediterranean countries and elsewhere, and of herbarium specimens of Recent dasyclads from the warm seas of the Atlantic, Indian and Pacific Oceans. Dasyclad morphology, methods of study of fossil dasyclads, and the limitations of such material, are outlined, and the principles of classification employed are examined. The results are applied to the Middle East flora ; about 80 species, referred to 39 genera and 12 tribes of the family, are described and figured or discussed. Included are a small minority of fossils whose dasyclad nature is uncertain or which have been incorrectly described as dasyclads, and a few Dasycladaceae *incerta sedis*. Stratigraphically the general agreement of the Middle East dasyclad floras with those of Europe and elsewhere is confirmed, though differing local ranges for certain Upper Jurassic–Lower Cretaceous species are detailed. Geographically the homogeneity of the Tethyan dasyclad floras from west to east is confirmed at most stratigraphic levels ; the Middle East forms a central sector of this latitudinal belt. In the Palaeocene, evidence of the mixing of eastern and western elements in the Middle East area is noted. Ecologically the evidence of all the Middle East fossil dasyclads is in accord with what is known of their living descendants.

Finally, from an evolutionary point of view, the most important points of detail are the

interpretation of a Palaeocene genus as possibly having been similar to the atypical living *Dasycladus* in shedding gametes direct instead of by the usual dasyclad encystment, and in the conclusion that the terminal umbrella-type fertile discs seen in the living *Acetabularia* may be of different origin though of similar morphology in the fossil *Clypeina*. Also described is a species of *Cymopolia* showing the actual transition from cladospore to choristospore organization. The views of Julius Pia on the general course of dasyclad evolution are confirmed. No detailed explanation of this evolution can be offered, but the decline of dasyclads in abundance and importance throughout geological time, and their replacement by certain calcified Codiaceae in this respect, are now considered to be due to the differing relation of calcification to reproductive bodies in the two families, this itself probably due to their differing basic morphology.

I. INTRODUCTION

PRESENT-DAY dasyclads are small single-cylindrical segmented or umbrella-shaped green algae, calcified in varying degree, and occurring mostly in warm very shallow waters in tropical and sub-tropical seas. The family is not a large one in number of component genera, and many of these illustrate markedly the phenomenon of discontinuous distribution. *Neomeris*, for example, is largely divided in occurrence between the East and West Indies. When the fossil record is examined, the relict nature of the Recent survivors is seen at once. Ancestral forms range from the lower Palaeozoic onwards, and show a variety of strange genera now extinct. At some geological levels they occur in profusion over large areas, and are used as index fossils. Although individual sizes are small, when compared with those of some other marine algae, yet proportionally giant forms occur amongst the fossil dasyclads, and the Lower Carboniferous *Koninckopora* has been estimated to have attained a length of 50 cm. This phenomenon of former large size is also not uncommon with relict groups.

In the largely arid land-area now known as the Middle East a thick succession of ancient sediments bears witness to the former occurrence there of the old Tethyan Sea. From Upper Palaeozoic to Mid-Tertiary times conditions of repeated shallow, warm-water, limy-bottomed shelf-areas afforded suitable environments for the growth of calcareous algae, and although, palaeontologically speaking, collections are rudimentary compared with those from Europe, yet examination of routine stratigraphical samplings has shown a succession of algal floras. In these the largest single group, taxonomically if not numerically, is the Dasycladaceae. Although they do not form whole reef-like rock-masses as do the Corallinaceae, nor occasion a monotonously distinctive rock-type as do the sand-like fragmentary remains of the Chaetangiaceae, yet the dasyclads impress themselves upon the mind of the student by the seemingly endless variety of structures, all based on a common plan. In their evolution, as interpreted by the Viennese worker Julius Pia over a working lifetime of thirty years, largely from European materials, there may be traced a progressive elaboration of their verticils or whorls of side-branches, the reproductive structures moving from within the stem-cell, first to within the side-branches, and then to specialised outgrowths adjacent to the subsidiary branches. But superimposed on this was a variability of calcification, as between one genus and another, and apparently showing no progressive trend throughout geological time. Some, heavily calcified, show hollow moulds of almost the whole set of branching structures

in the plant and the fossil leaves no doubt, when well-preserved, of the state of evolution attained. Others calcify daintily and capriciously, each consistent for its genus, but anywhere between the stem-cell and near the tips of the finest outer branches. Both of these extremes are known ; and whilst distinctive enough both morphologically and stratigraphically, leave doubt as to what pattern of dasyclad alga formed them, and where it should be placed within the family.

Middle Eastern Dasycladaceae were originally studied by me for their stratigraphic value, as explained below, and hence largely by comparison with those from elsewhere. In rock collections made for general survey purposes, rather than primarily for the amassing of good algal material, and showing frequently poor preservation, many occurrences have come to light which otherwise would have remained unknown, whilst on the other hand some of these specimens remain tantalisingly incomplete for palaeobotanical study. Nevertheless it may be said here that the Middle East mirrors and sometimes supplements the European record of dasyclad evolution from Permian to Eocene. Apart from very many points of detail, such as additional genera or species, extensions of generic range, and the filling in of geographical species-occurrences between East and West, there are several discoveries of especial interest, confirming earlier hypotheses or offering evidence for the probable ancestry of well-known genera.

The present work originated as part of a study of the calcareous algae generally of the Middle East, undertaken as part of my duties for Iraq Petroleum Company Ltd. Commissioned early in 1953 by Dr. F. R. S. Henson, then in charge of the Company's geological research activities, it was undertaken as a section of a project for elucidating the stratigraphical value for economic purposes of microfossil groups other than the foraminifera, and the results in this direction has been summarized elsewhere (Elliott, 1960). Many tens of thousands of thin-sections, prepared from well and surface samples, have been examined, as well as large quantities of rock and sand samples. This material came primarily from Iraq, Qatar, Oman and the Hadhramaut, where Iraq Petroleum and its associated companies operated, but much comparison material from the countries bordering the Mediterranean, and from the remainder of the Middle East, has been examined also, as well as Recent algae in the collections of the British Museum (Natural History) and elsewhere. Of those within the Company who have sent me dasyclad material for study, my thanks are offered to Messrs. H. V. Dunnington, E. Hart, D. M. Morton, K. al Naqib, A. J. Standring, W. Sugden, R. Wetzel, E. Williams-Mitchell, and Drs. R. C. van Bellen, Z. R. Beydoun, M. Chatton, and T. Harris. Of my many French friends and correspondents, I would single out for especial mention Professor J. Emberger, formerly of Algiers, who in exchanges has sent me many fine dasyclad rock-samples from the North African sector of the Tethys. At the British Museum (Natural History) members of the staffs of both Botanical and Palaeontological Departments have afforded me every facility, and I remember with gratitude the kindness and interest of the late W. N. Edwards, former Keeper of the latter department. Thanks are due to all those who have corresponded with me on dasyclad matters, from all over the world and too numerous to list here. Mr. R. C. Miller, when Senior Tech-

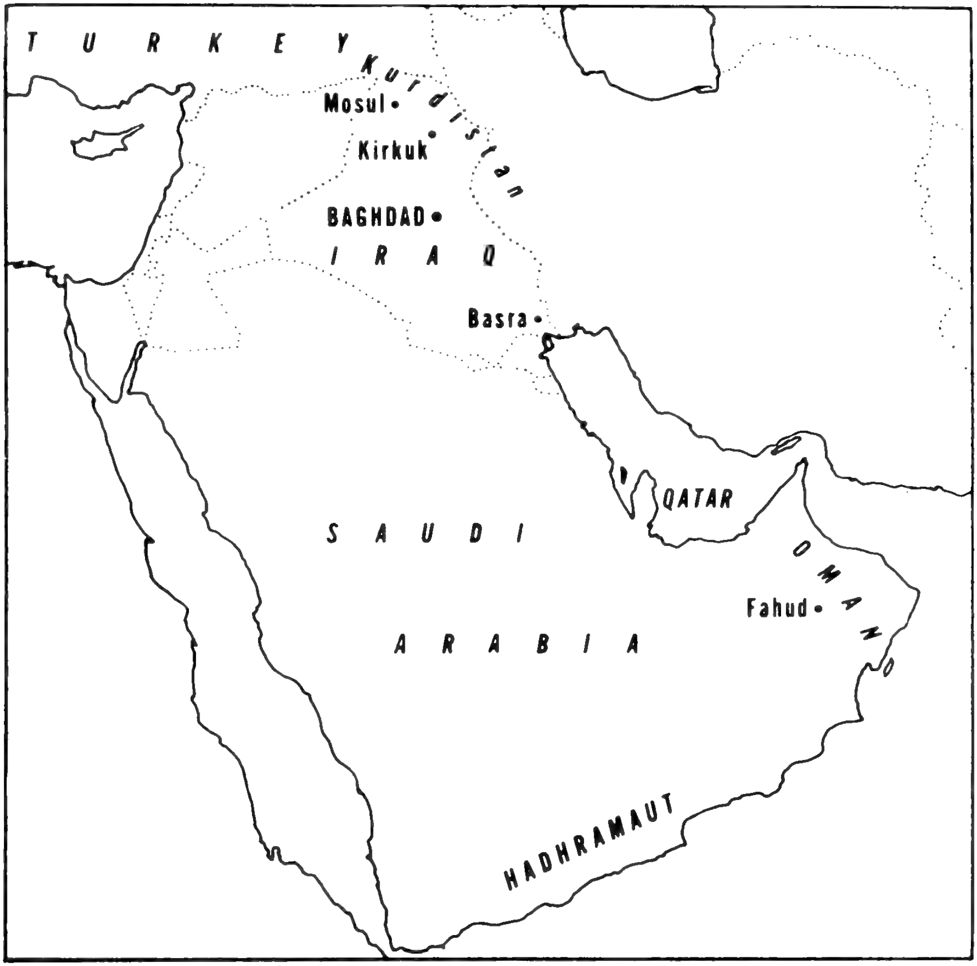
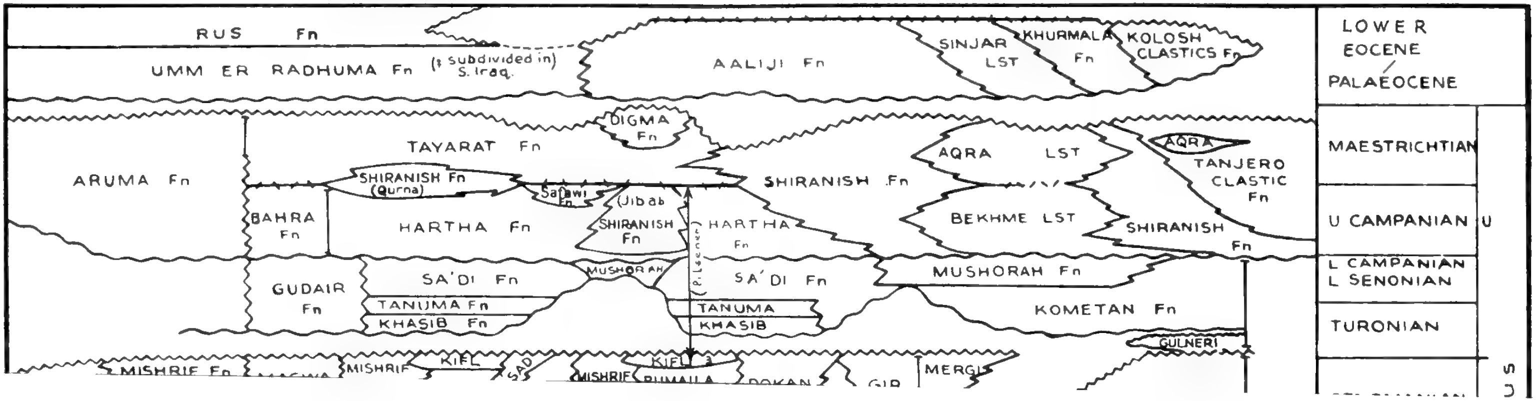


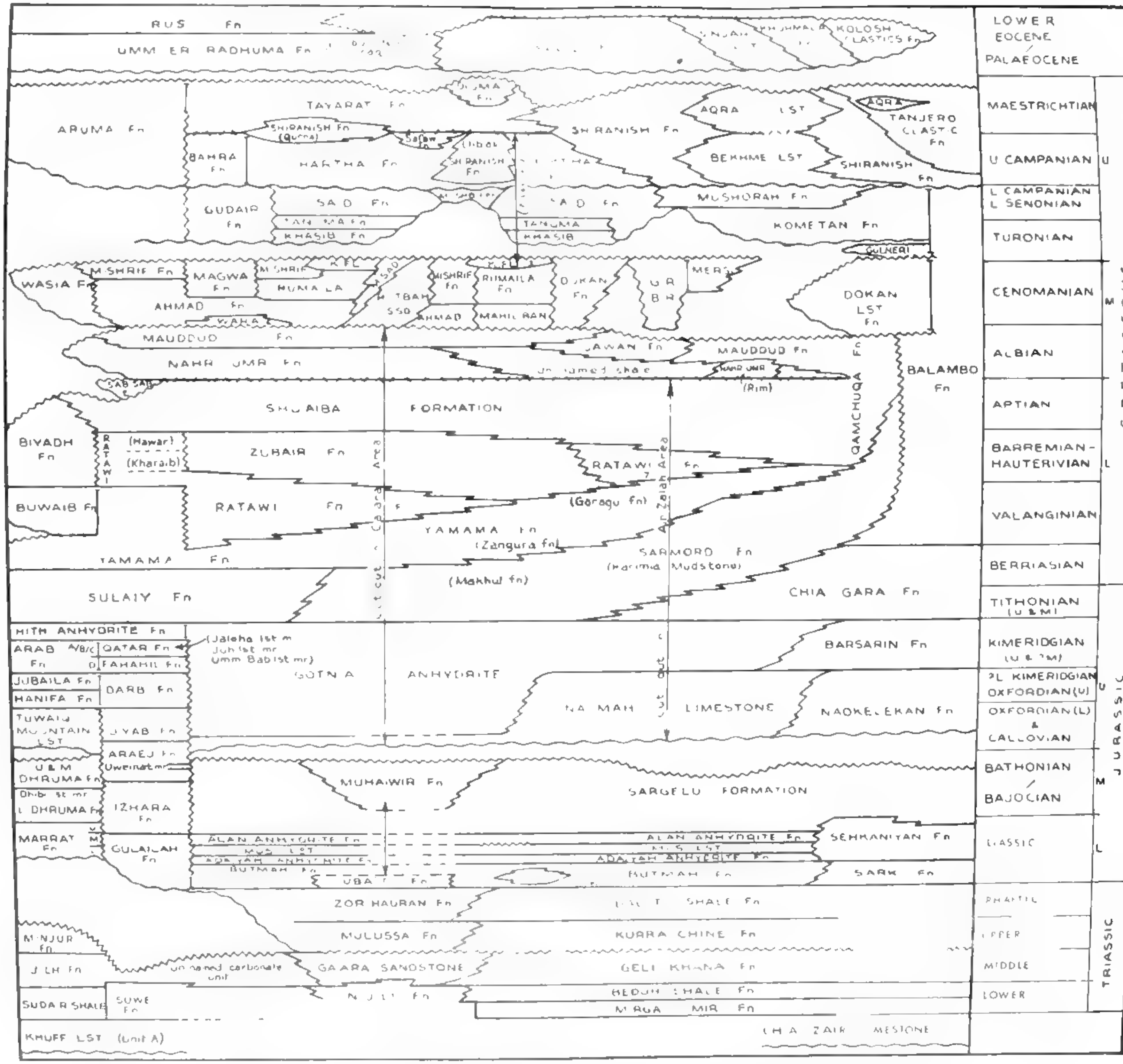
FIG. 1. Sketch-map of the Middle East, showing areas of provenance of principal collections examined.

nician at Iraq Petroleum's London headquarters, several times provided me with good transverse and longitudinal sections of dasyclads no larger than a few millimetres of fine pencil-lead, and Mr. J. Pope, of the Company's Photographic Department coped admirably with the problems of microphotography of largely monochromatic thin-sections : I thank them both. The distribution-maps and range-charts were prepared in Iraq Petroleum's Prodex Drawing-Office, and my thanks are due to Mr. E. G. Field and his staff for their services.

At Reading University, where these studies were continued and the present work offered as a thesis for the degree of Ph.D., I am especially grateful to my supervisors, Professor P. Allen, Dept. of Geology, and Professor T. Harris, Dept. of Botany, for



LOWER EOCENE / PALAEOCENE
MAESTRICHTIAN
U CAMPANIAN
L CAMPANIAN
L SENONIAN
TURONIAN
U
RUS Fn
UMM ER RADHUMA Fn (± subdivided in) S. Iraq.
AALIJI Fn
SINJAR LST
KHURMALA Fn
KOLOSH CLASTICS Fn
ARUMA Fn
TAYARAT Fn
DIGMA Fn
SHIRANISH Fn (Qurna)
Safawi Fn
(Jibab SHIRANISH Fn
SHIRANISH Fn
AQRA LST
BEKHME LST
AQRA
TANJERO CLASTIC Fn
SHIRANISH Fn
BAHRA Fn
HARTHA Fn
HARTHA Fn
(P. Lsener)
GUDAIR Fn
SA'DI Fn
TANUMA Fn
KHASIB Fn
MUSHORAH
SA'DI Fn
TANUMA
KHASIB
MUSHORAH Fn
KOMETAN Fn
GULNERI
MISHRIF Fn
MISHRIF
KIFL
KIFL
MISHRIF
DOKAN
GIR
MERGI



LOWER EOCENE / PALAEOCENE
MAESTRICHTIAN
U CAMPANIAN
L CAMPANIAN L SENONIAN
TURONIAN
CENOMANIAN
ALBIAN
APTIAN
BARREMIAN-HAUTERIVIAN
VALANGINIAN
BERRIASIAN
TITHONIAN (U & M)
KIMERIDGIAN
OXFORDIAN (L) & CALLOVIAN
BATHONIAN / BAJOCIAN
LIASSIC
LOWER
MIDDLE
CRETACEOUS
JURASSIC
TRIASSIC
RUS Fn
UMM ER RADHUMA Fn
KOLOSH CLASTICS Fn
TAYARAT Fn
ARUMA Fn
SHIRANISH Fn
AQRA LST
TANJERO CLASTIC Fn
BAHRA Fn
HARTHA Fn
BEKHME LST
SHIRANISH Fn
GUDAIR Fn
SAD Fn
TANUMA Fn
KHASIB Fn
MUSHORAH Fn
KOMETAN Fn
GULNERI
MISHRIF Fn
MAGWA Fn
WASIA Fn
AHMAD Fn
RUMAILA Fn
MAHILBAN
DOKAN LST Fn
MAUDDUD Fn
NAHR UMR Fn
JAWAN Fn
BALAMBO Fn
SHUAIBA FORMATION
QAMCHUQA Fn
BIYADH Fn
ZUBAIR Fn
RATAWI Fn
BUWAIB Fn
YAMAMA Fn
(Zangura fn)
(Garagu fn)
SARMORD Fn
(Karimia Mudstone)
SULAIY Fn
(Makhul fn)
CHIA GARA Fn
HITH ANHYDRITE Fn
ARAB Fn
QATAR Fn
FAHAHIL Fn
(Jaleha lst mr, Juh lst mr, Umm Bab lst mr)
GOTNIA ANHYDRITE
BARSARIN Fn
JUBAILA Fn
HANIFA Fn
DARB Fn
NAJMAH LIMESTONE
NAOKELEKAN Fn
TUWAIQ MOUNTAIN LST
ARAEJ Fn
Uweinat mr
DHRUMA Fn
IZHARA Fn
MUHAIWIR Fn
SARGELU FORMATION
MARRAT Fn
GULAILAH Fn
ALAN ANHYDRITE Fn
MUS LST
ADAIYAH ANHYDRITE Fn
BUTMAH Fn
SEHKANIYAN Fn
SARKI Fn
UBAID Fn
ZOR HAURAN Fn
KURRA CHINE Fn
MINJUR Fn
MULUSSA Fn
GAARA SANDSTONE
un named carbonate unit
GELI KHANA Fn
BEDUH SHALE Fn
MIRGA MIR Fn
SUDAIR SHALE
SUWE Fn
KHUFF LST (Unit A)
CHIA ZAIRI LIMESTONE

their help and encouragement, and their very real interest in the project. Also my thanks go to my fellow-students with whom I have had many interesting discussions, and to the staff of the Sedimentological Laboratory for services of all kinds.

Finally, I would acknowledge my indebtedness to the Management of Iraq Petroleum Company, Ltd., who generously agreed to and made possible this liaison between academic and economic geology. Dr. C. Thiebaud, Exploration Manager, and Mr. H. V. Dunnington, Chief Geologist, who approved and submitted the project, I thank sincerely and gratefully for their efforts on my behalf. All the material in this paper has been presented to the British Museum (Natural History).

II. STUDY AND CLASSIFICATION OF FOSSIL DASYCLAD ALGAE

Modern views on the botanical classification of dasyclad algae, their relationship to other green algae and the precise systematic status to be accorded them, may be found in Fritsch (1935) and more recently in Egerod (1952). Such work is necessarily based on the detailed study of structure, development and reproduction in the living plant. All the fossil forms described in this work are referred to a single family, the Dasycladaceae. Within this family the subclassification into tribes has been largely the work of palaeontologists, especially J. Pia, since the fossil forms are so numerous. Pia's classification appeared in the 1920s (Pia 1920 ; 1927) and was followed with slight modification and comment by later workers including Emberger (1944), Johnson (1954a ; 1961b) and Kamptner (1958).

Whilst it cannot be over-emphasized that as a general rule the fullest understanding of fossils is only to be obtained from an understanding of their living descendants, where skeletal structures can be studied functioning with the associated organic tissues missing in the fossil, yet much depends on how much is preserved in the latter, and how well it is preserved. In Recent members of the red algal family Chaetangiaceae, it was concluded by Svedelius (1953) that experimental spore-culture was necessary for conclusive pairing of the morphologically distinctive sexual and non-sexual generations. A morphological classification is thus inevitable with the fossil Chaetangiaceae, which in addition are notoriously fragmentary. For this general reason the account of dasyclad structure set out below stresses those structures and features of the plant which are of assistance in an understanding of the calcified remains found fossil.

Individual living dasyclads are usually small, vertically-growing algae : one observer described them as resembling " little green sausages " (Church 1895). Attached at the base by a rhizoid or holdfast, the core of the plant is a proportionally long cylindrical stem-cell, extending from rhizoid to apex. From this, whorls or verticils of lateral branches are given off at successive closely-set levels : these branches may themselves divide more than once, and they also bear the sporangial bodies. Much of the plant above the rhizoid is crusted with calcium carbonate.

The commonest fossils of dasyclads are thus small calcareous hollow cylinders with tubular pores and cavities in the thickness of the wall, the pattern of pores and cavities occurring again and again at successive levels in the wall-thickness along the cylinder. The main central tunnel represents the stem-cell, the branching tubular

pores the lateral branches and the cavities the sporangia. There may be a terminal "pepper pot" structure at the apex. Determination of the fossil is made on the detail, number, arrangement and size of these structures. The essential preparations are a longitudinal cut or thin-section through the long central cylinder-axis, and a transverse section at right angles to this. More than one of the latter may be required when the lateral branches are strongly inclined relative to the horizontal plane. A whole, three-dimensional specimen, or at least a weathered surface to show surface-detail, is desirable for describing new material. A selection of such loose specimens for the preparation of orientated sections is ideal, but not always available. Once the essential structure is understood, the species may be recognized with practice in all manner of random oblique or tangential cuts. It should be noted that in exceptionally large dasyclads individual longitudinal and transverse sections, even if correctly orientated, may pass between verticil-detail and so not be diagnostic.

Exact measurements of the dimensions of thallus, stem-cell, branch- and sporangial-detail are desirable in describing dasyclad algae. It should, however, be remembered that whilst species do show average size and proportions of both thallus and component structures, they are plants and, like all plant life, variable. Dimensions are therefore a guide and not an exact character in dasyclad taxonomy.

A considerably greater variety of form has existed in dasyclads through geological time than survives at the present day. The notes which follow deal with the principal types which occur.

The stem-cell may be thin- or thick-cylindrical, club-shaped with either gradual increase of diameter or bulbous termination or greatly swollen, even to a near-spherical shape. Normally it is represented in fossils by a simple central mould, but certain cylinders whose walls are formed by hollow spherical calcareous bodies, adjacent, touching or fused, e.g. *Atractyliopsis*, are interpreted as remains of dasyclads in which the sporangia were within the stem-cell itself and calcified as a sub-dermal stem-cell peripheral zone to give the fossil seen. Occasionally there is some doubt as to whether a calcareous filling between these bodies occurred during the life-time of the plant, in the lower, older part, or is a post-mortem mineralisation feature (e.g. *Aciculella*).

Exceptional forms in which the stem-cell is creeping in habit, or modified into a thin support for a large terminal disc or discs, are dealt with separately below.

The lateral branches have been described above as occurring at successive horizontal levels in whorls or verticils. Pia (1920) recognized a tripartite classification of their relationship to the stem-cell. In the more primitive aspondyl type the pores marking the origin of branches occur irregularly, more or less over the whole stem-cell surface. In the euspondyl type single branches are set in approximately horizontal whorls, whilst in the metaspondyl arrangement tufts of branches originate from the pores of the verticils.

The lateral branches themselves may be single structures, or more commonly branched, so giving primaries, secondaries, tertiaries etc. The number of sub-branches at each point of branching or division is approximately constant within the species. These points of branching are constricted and there also occur genera in

which constriction of the individual branches and branchlets occurs without division at these constrictions e.g. *Palaeodasycladus*.

The reproductive structures, usually termed sporangial cavities in the fossil literature, are often conspicuous features of the branch-detail, and are of great value in classification. They may be completely encased in the calcareous coating where this is well-developed, and indeed, in most similar living forms, gametes are only set free from resting cysts on the eventual post-mortem break-up of the calcareous structures. General classification of the condition seen in fossils is again tripartite and due to Pia. The endospore type is presumed to have had reproductive elements within the stem-cell. This is characteristic of the Palaeozoic and only such forms as the doubtful *Atractyliopsis* already mentioned and a species of *Diplopora* show any direct structural evidence of this condition. In the cladospore type, dominant throughout most of the Mesozoic, the reproductive cavities are considered to have been within swollen lateral branches. Finally, in the choristospore type the reproductive elements are located in special outgrowths, usually well-calcified, from the lateral branches. Commonly they are attached at the division of primaries into secondaries (e.g. *Cymopolia*) but various other positions characterise other genera. This type ranges from Cretaceous to Recent. Rezak (1959a) has drawn attention to the parallel between Pia's view of the migration of reproductive elements during phylogeny from stem-cell to lateral sporangia, and Egerod's summary (1952) of the migration during ontogeny of the dividing nucleus from the holdfast of the vegetative thallus into the gametangial rays of the reproductive thallus. Recent studies of the genetic mechanisms involved in this latter phenomenon in the living *Acetabularia* (Brachet 1965), do not invalidate this comparison. Summary of the chromosome mechanisms in the Dasycladaceae (Puiseux-Dao 1966) emphasizes their distinctiveness amongst green algae.

There exists a minority of dasyclads which depart from the usual pattern of a vertical calcareous cylinder described above.

Vermiporella and the somewhat doubtful *Pseudovermiporella* from the Palaeozoic are recumbent–irregular in form, indicating a presumed creeping thallus in life. The former branches, and the latter shows a peculiar double calcareous structure in part of the thallus. This is dealt with fully in the systematic descriptions below.

In the Palaeozoic *Mizzia* and certain later genera the stem-cell occurred as consecutive bead-like structures, almost always dissociated as found fossil. Certain Tertiary dasyclads (e.g. *Larvaria*) were of normal tubular pattern but the verticils came apart after death and usually occur fossil as separate ring-like structures.

Another and commoner growth form is where the plant appears with a thin, lightly-calcified stem supporting a specialized flower-like disc or series of discs, usually found separate as fossils, in which the radial segments or " petals " are calcified structures containing the reproductive elements in life (e.g. *Clypeina*). In *Acicularia* these segments themselves came apart after death and occur as separate microfossils, of varying form, known as spicules. Not all such spicules, however, have this origin : some, such as the Tertiary *Carpenterella*, are believed to be dissociated structures from the interiors of dasyclads of modified cylindrical form.

Calcification

During individual development recent dasyclads pass through several growth stages : calcification begins fairly late, often being initiated around the early reproductive structures, and thus it is the adult plant of which a fossil record is possible. Occasionally exceptional fossils, such as the Cretaceous *Trinocladus*, show differences in detail between the lower, earlier formed whorls and the upper, later ones, both being calcified. However, a combination of capriciousness in degree and occurrence of calcification for the members of the family viewed together, and constancy for the calcification of the individual species, is the rule in the Dasycladaceae.

Consequently, the reconstructions possible of the plants which originated the calcareous fossils vary enormously. With heavy calcification a record is preserved of the stem, branch and sporangial details, and also the outline of the whole plant, only the finest branchlets projecting further during life. With those which calcify, but come apart after death, a fair degree of reconstruction is possible, and chance preservation of rare complete specimens illuminates the common segments or debris. Where calcification is confined to a narrow zone, either close to the stem-cell as in *Pagodaporella*, or between the tips of the branchlets only, as with *Tersella*, the details of the plant will probably always be doubtful. Finally, such odd remains as *Aciculella*, already mentioned, or tiny dissociated elements like *Terquemella*, render necessary the description of form-genera whose components may be of diverse origin and whose position within the family is unknown.

List of Middle Eastern Fossil Dasycladaceae

In the list below, those genera of dasycladaceae recognized in the course of the present work are set out under the appropriate " tribes ", or subdivisions of the family. These tribes, proposed by Pia (1920 ; 1927), have been followed and modified by later workers, notably in the comprehensive schemes of Emberger (1944) and Kamptner (1958) while other workers, elements of whose classifications have been especially considered here, are Morellet (1922), Johnson (1954a ; 1961b) and Rezak (1959a).

Classification of this kind is based on structure as preserved in the fossils, and on phylogeny, which may be regarded in this connection as interpreted structure. The student of phylogeny assigns values to elements of structure in accordance with his or her experience of the group studied. Close similarities and near-identity, particularly of external form and gross structure, are often discounted in favour of smaller and less obvious features. These latter are valued on account of their persistence throughout time or their alleged significance as early or late manifestations of distinctive structures in related members of the group. In general, this interpreted structure determines the taxonomic category allotted. However, the success of a group, evidenced by numerical abundance of individuals and extensive minor variation from a common structure, as opposed to rare, but profound deviation which were evidently biologically unsuccessful or unfortunate, often leads to a taxonomic up-grading of the group being classified.

Such classification, with its very different allocation of importance to the same or

similar structures in related groups, reflects attempts towards a real understanding of evolution, and dissatisfaction with rigid morphological classification, however logically contrived. The subjective elements in such reasoning, normally subordinate, become much more apparent when subdivision is attempted of a relatively homogeneous biological group. In the " small change " of evolution personal choice in detailed classification becomes obvious. Thus *Clypeina* has been referred both to the Diploporeae (Pia 1927, Emberger 1944) and to the Acetabulareae (Morellet 1913 ; 1922 ; 1939 ; Rezak 1957). Since clypeiniform remains are now recorded from the Permian (p. 36) it seems possible that the different morphological trends seen in dasyclads may have evolved more than once, and the classification of such similar forms is difficult. In the present work *Clypeina* is placed in the new tribe Clypeineae : the reasons for this and the relationship of the genus to *Actinoporella*, here left in the Diploporea, are discussed below (p. 99).

In the Dasycladaceae considered here, the increasing complexity of branch-structure, and transference of position of reproductive structures already mentioned, are noticeable evolutionary trends. It is inevitable, however, that in classifying fossil genera represented by very varied results of superimposition of localized calcification on different stages of these trends, that frequently some uncertainty should be felt as to the appropriate tribe. The Middle Eastern genera and species described below have been so referred in accordance with literature quoted. For many genera, simple or complex, e.g. *Diplopora* or *Neomeris*, there is no uncertainty. For others, e.g. *Atractyliopsis* or *Griphoporella*, the nature of the fossil ensures its relegation as *incerta sedis*. Between these extremes are several doubtful cases, assigned here to a tribe for consistency, in accordance with published accounts ; e.g. *Cylindroporella* to Diploporeae (Kamptner 1959) and *Terquemella* to Dactyloporeae (Morellet 1922 ; Emberger 1944). *Pagodaporella* is assigned to Dasycladeae, in view of its analogy with *Dasycladus*. *Mizzia* is placed under Diploporeae following Rezak (1959b), and *Acroporella* also, in view of its author's opinion on its relation to *Salpingoporella* (Praturlon 1964). The writer is in agreement with the need for subdivision of the Diploporeae expressed by Rezak (1959a : 125), but has not attempted this, still less general reclassification of dasyclad tribes, in the present study of Middle East representatives of the family. The recent discovery of a *Dissocladella* in the older Mesozoic (Ott 1965), and the phylogenetic considerations given by this writer, show how random and incomplete is the evidence for major re-classification.

The table given, therefore, represents current conventional taxonomic assignment of the genera listed, which are dealt with alphabetically in the main descriptive part of the work, where the synonymies are selected to cover primary descriptions, revisions and Middle East occurrences only.

Family **DASYCLADACEAE** Kützing 1843
orth. mut. Hauck 1884

Tribe **DASYPORELLEAE** Pia 1920
Anthracoporella

Tribe **CYCLOCRINEAE** Pia 1920
Epimastopora
Pseudoepimastopora

Tribe **DIPLOPOREAE** Pia 1920
Acroporella
Actinoporella
Cylindroporella
Diplopora
Gyroporella
Macroporella
Mizzia
Munieria
Permoperplexella
Pianella
Salpingoporella

Tribe **TEUTLOPORELLEAE** Pia 1920
Teutloporella

Tribe **TRIPLOPORELLEAE** Pia 1927
Triploporella
Broeckella

Tribe **THYRSOPORELLEAE** Pia 1927
Belzungia
Dissocladella
Thyrsoporella
Trinocladus

Tribe **CONIPOREAE** Pia 1920
Palaeodasycladus

Tribe **CLYPEINEAE** (trib. nov. ; see p. 99)
Clypeina

Tribe **DACTYLOPOREAE** Pia 1927
Terquemella

Tribe **DASYCLADEAE** Pia 1920
Pagodaporella

Tribe **NEOMEREAE** Pia 1920
Cymopolia
Indopolia
Karreria
Larvaria
Neomeris

Tribe **ACETABULARIEAE** Pia 1920
Acicularia

DASYCLADACEAE *incerta sedis*

Atractylopsis
Furcoporella
Griphoporella

Problematica, possibly dasycladaceae

Pseudovermiporella (?**DASYPORELLEAE**)
Hensonella (?**DIPLOPOREAE**, as *Salpingoporella dinarica*)

Algae, not dasycladaceae

Thaumatoporella
" *Epimastopora minima* Elliott " (= *Tauridium* sp.)
" *Griphoporella arabica* Pfender "
(= *Ovulites maillolensis* Massieux).

III. SYSTEMATIC DESCRIPTIONS

In the descriptions which follow, the geological ages of all material mentioned are given in terms of local rock-units and standard international stages as far as possible. Every effort has been made to take account of all relevant literature up to the end of 1966. A bibliography of the geology of the Middle East is far outside the scope of the present work, but key publications may be quoted for Iraq, Qatar, Oman and the Hadhramaut from which the vast majority of the specimens were collected. For Iraq, the very detailed Lexique Stratigraphique International, listed in the present bibliography both under Bellen, R. C. van (1959), and under Dunnington, Wetzel & Morton (1959), is invaluable. The Hadhramaut material is similarly covered by Beydoun (1964). A suitable account for the much smaller and simpler Qatar is that by Qatar Petroleum Company, Ltd. (1960). Oman is covered by the general account of Morton (1959), and the detailed local papers of Hudson and collaborators are mentioned where relevant in the present study.

The regional location of the numerous small localities quoted are best gleaned from these works ; in the present text they are given with the appropriate province or administrative division. The geographical co-ordinates of these localities are listed on p. 109.

Genus *ACICULARIA* (d'Archiac) Munier-Chalmas

Diagnosis. Calcareous spicules, typically elongate-cuneiform, circular or flattened in cross-section, set peripherally with small spherical cavities ; in life part of the fertile whorl of the plant.

Acicularia was proposed by d'Archiac (1843 : 386) for certain fossil spicules occurring in the Paris Basin Eocene. Referred to different animal groups by various authors, their algal origin was recognized by Munier-Chalmas (1877), and the subsequent discovery of a living species confirmed this diagnosis. Munier-Chalmas published little but the bare statements of this and other original discoveries, and the details of his species, and the subgenus *Briardina*, are to be found in later authors, notably in the classic works of L. and J. Morellet (1913, 1922), and in the paper by

Costantin (1920) which gives some of Munier-Chalmas' original figures. The recent *Acicularia* has been merged as a section *Acicularioides* of *Acetabularia* (Egerod 1952), but in the fossil state at least the remains are distinctive and the name a useful one.

Acicularian spicules are typically small elongate needle-like calcareous bodies, derived from the specialized fertile disc of the plant and containing tiny spherical sporangial cavities. (Somewhat similar discoidal or spherical bodies, *Terquemella* of Munier-Chalmas were recognized by the Morellets as sporangial structures from the walls of fossil Bornetelleae (= Dactyloporeae), which are of normal tubular dasyclad pattern and not umbrella-shaped like *Acicularia* or *Acetabularia*). Both morphological types of spicule are known from the Jurassic onwards. Whilst the attribution of the Tertiary species is as given above, the origin of the Mesozoic forms is much more doubtful. Pia (1936a, b) has described Cretaceous spicules which he referred to *Acicularia* but considered might indicate a connection between *Acicularia* and *Terquemella*, obviously using the latter in a strictly morphological sense.

In the Middle East true *Terquemella* spp. occur in the Palaeocene-Lower Eocene ; these species are dealt with below under *Terquemella*. The remaining *Acicularia* spp. are now described here.

Acicularia antiqua Pia

(Pl. 1, figs. 1, 3)

1936a *Acicularis antiqua* Pia : pl. 3, figs. 1–14.
1955b *A*. cf. *antiqua* Pia ; Elliott : 126.

Description. Rounded, cuneiform, calcareous bodies, circular or ovoid in cross-section, containing numerous submarginal spherical hollows (sporangial cavities). Length up to 0·780 mm., with maximum diameter of 0·364 mm. The sporangial cavities are consistently about 0·040 mm. in diameter, and in thin-section appear set apart by their own diameter or a little more along the margins of the spicules.

Horizon. Cretaceous of North Africa and the Middle East.

Material. Seen in thin-section from the subsurface Garagu formation (Valanginian) of Kirkuk well No. K 116 (Kirkuk Liwa, Iraq), from the Sarmord and Qamchuqa formations (Neocomian and Aptian-Albian) of the Surdash district (Sulemania Liwa, Iraq), from the Upper Musandam formation (Lower Cretaceous, Barremian-Aptian) of the Hagab area, Oman, Arabia, and from the Maestrichtian of Diza, (Erbil Liwa, Iraq).

Remarks. Random sections of acicularian spicules are not uncommon at many levels in the Middle East Cretaceous. With few exceptions, they may be divided into two classes, on the size of the sporangial cavities. The smaller, always set in a circular section indicating a spherical spicule, is described elsewhere under *Terquemella* s.l. The larger, described above, occurs in a variety of random cuts suggesting a rounded–cuneiform spicule. For this form Pia's *Acicularia antiqua* (Pia, 1936a) appears to be available. The type material, from the Cenomanian of Libya, Northern Africa, is described as probably wedge-shaped or pointed, length probably not exceeding twice the thickness, greatest diameter 0·330 mm., diameter of spore-

cavities 0·040–0·055 mm., and not curved or hooked as in *A. dyumatsenae* Pia from the Indian Danian (Pia 1936b). The Middle Eastern material, on the basis of the few available dimensions and characters, seems to vary little beyond this, and the name is adopted. A few examples from the subsurface Garagu of Kirkuk show exceptional sporangial diameters of 0·065 mm., but they occur in random transverse cuts only. *A. endoi* Praturlon (1964), from the Italian lower Cretaceous, is described as a spicule, slightly larger with larger sporangial cavities, which however are more regularly and peripherally arranged to give a starred appearance in thin-section.

A. antiqua is more common in Lower than Upper Cretaceous in my experience, but ranges from bottom to top of the system. If the spicules are the remains of more than one botanical species in this long period, there is no apparent evidence of this in the microfossils as preserved. They should not be confused with the micro-problematicum *Coptocampylodon* (Elliott 1963a) which resembles an acicularian in transverse cut, but is readily distinguishable by the longitudinal sections normally associated.

?***Acicularia elongata*** Carozzi

1947 *Acicularia elongata* : Carozzi : 13, figs. 1–8.

REMARKS. Carozzi's species, from the Swiss Upper Jurassic, is a distinctively elongate spicule of rather ragged outline. In the Upper Jurassic of Jabal Kaur, Oman, Arabia, remains occur which are possibly of the Swiss species, but are not well enough preserved to permit of a positive reference. They are associated with *Pianella gigantea* Carozzi and the microcoprolite *Favreina salevensis* (Paréjas), also described from the Swiss Upper Jurassic.

Acicularia (Briardina) sp.

(Pl. 1, fig. 6)

1913 *Acicularia* section *Briardina* Munier-Chalmas ; L. & J. Morellet : 33.

REMARKS. In the Palaeocene Limestones of the Batinah Coast, Oman, one or two examples of a small acicularian apparently referable to this section or subgenus have been noted. The best shows in longitudinal thin-section as a needle or narrow wedge-shaped spicule, 1 mm. long, 0·22 mm. wide at the outer end and slightly hooked at the inner (pointed) end : the sporangia are 0·078 mm. in diameter, in a double row, narrowing to a single on the upper face. The section cuts at the thinner end through the sporangia of the lower face, the elongate spicules of species of *Briardina* being thin, with flat or slightly concave upper and lower surfaces.

This may be the earliest representative of the subgenus, the Paris Basin species being Lutetian or later in age (Morellet 1913, 1922), and the acicularians from the Montian (Morellet 1940) not being referred to the subgenus.

Genus ***ACROPORELLA*** Praturlon 1964

DIAGNOSIS (after Praturlon). " Not segmented **DASYCLADACEAE** having

simple, long, not ramified, akrophorous branches. Reproduction probably endospore ". " The branches are namely by no means ' gegen aussen deutlich erweitert ', as in *Salpingoporella, Pianella, Macroporella,* as well as do not incline to shut outwards as in *Oligoporella*. They are namely intermediate between the two types ". (Praturlon 1964 : 177).

Acroporella assurbanipali sp. nov.
(Pl. 1, fig. 5)

1960 *Macroporella* sp. ; Elliott : 222.

Description. Cylindrical tubular calcified dasyclad, external diameter 1·36 mm., internal diameter 0·55 mm. (40% of external) ; successive near-horizontal verticils, probably 3 or 4 per mm. of tube-length, of perhaps twelve radial branches each. The single branches communicate with the stem-cell cavity by a pore of about 0·052 mm. diameter : they then swell out to a fig- or flask-shaped cavity of 0·182 mm. maximum diameter, narrow to a slightly curved tube of 0·078 mm. diameter, and at the outer surface flare out to a shallow terminal diameter of 0·156 mm.

Horizon. Subsurface Lower Cretaceous of Iraq.

Holotype. The specimen figured in pl. 1, fig. 5 from the subsurface Garagu Formation (Valanginian-Hauterivian) of Kirkuk Well no. 116, Iraq. V. 52032.

Remarks. *Acroporella* Praturlon (type-species *A. radoicici* Praturlon 1964) is a primitive form from the Lower Cretaceous of Italy, apparently of somewhat intermediate branch-characters, though well figured and described by him. The Kirkuk specimen exactly fits his general diagnosis for branch-structure, rather better than the type-species, in fact, but the thallus shows more than double the dimensions of the Italian species, and the shape of the peculiar branches is unique. It is therefore made the type of a new species. The exact orientation of the curved branches relative to the cylinder-axis is difficult to make out from the long tangential section : the swollen portions may have housed the sporangia in life.

The specific name commemorates a king of ancient Assyria, within whose former boundaries Kirkuk now lies.

Genus ***ACTINOPORELLA*** Gümbel *in* Alth

Diagnosis. Verticils of several straight radial calcareous tubes, approximately in the same horizontal plane, separate for most of their length but meeting centrally in a calcareous ring, each hollow tube communicating by a single pore with the central cavity.

Actinoporella was created by Gümbel (Alth 1882), with type species *Gyroporella podolica* Alth (1878), which came from the Portlandian of Podolia (Cushman & Glazewski (1949) ; then in Austria, but subsequently in Poland and now included in the U.S.S.R.). This alga, represented by little impressions and hollow moulds of the verticils, was studied and reconstructed by Pia (1920 ; 1927) loose solid specimens from the same area have been seen by me. Each verticil shows numerous

radial tubes, slightly curved but approximately horizontal, about 20 in number, which are interpreted as the calcareous coatings or casings of simple primary side-branches. These are free for much of their length, but touch and become fused centrally, to form a circular ring through which the stem-cell passed. Pores on the inner surface of the ring mark the old communications of side-branches with stem-cell. A succession of such verticils built up in life the peculiar plant shown in Pia's reconstruction (fig. 2).

Subsequently Carozzi (1948) figured numerous thin-sections determined as *Actinoporella podolica*, from the Swiss Portlandian-Purbeckian. It is with these sections that the Middle Eastern material has been correlated, no solid individuals having been extracted. The commonest thin-section appearance is given by tangential cuts through the finger-like projections or side-branches, which show as chains of separate or touching circles. Less commonly vertical sections along the main axis show the central stem-cell and paired opposite side-branches, and rarely, transverse cuts show a whole disc or verticil.

Although locally common in the European Portlandian, and recorded from as low as Sequanian (Francois, Lehmann & Maync, 1958), this alga is characteristic in the Middle East of the Lower Cretaceous and has never been seen there in the Jurassic. In Italy (Sartoni & Crescenti 1962) it is recorded from both Tithonian and Valanginian-Hauterivian. It appears to be slightly more common in the Middle East at a Valanginian-Hauterivian level than in the Barremian-Aptian above (Elliott 1955b), but forms a noticeable constituent of the Middle Eastern " debris-facies " (Elliott 1958a), an off-shore accumulation of fine calcareous algal fragments in fire-grained sediments.

The relationship of *Actinoporella* to *Clypeina*, and their positions within the family Dasycladaceae, are discussed elsewhere (p. 99).

Actinoporella podolica Alth

(Pl. 1, figs. 2, 4, 7)

1878 *Gyroporella podolica* : Alth : 83, pl. 6, f. 1–8.
1882 *Actinoporella podolica* Alth : 322.
1920 *A. podolica* Alth ; Pia : 95, fig. 19, pl. 7, f. 1–7.
1948 *A. podolica* Alth ; Carozzi : 353, f. 49.
1955b *A. podolica* Alth ; Elliott : 126, pl. 1, f. 1.
1958a *A. podolica* Alth ; Elliott : 255, pl. 45, f. 1. pl. 47, f. 5.
1960 *A. podolica* Alth ; Elliott : 222, 223.

DESCRIPTION. Verticils of from 1·0 to 1·6 mm. or more total diameter, each consisting of a central calcareous ring with inner diameter of about 21% of the total diameter ; from this ring project 13 to 20 largely separate tubular elongate thin-walled cylindrical rays, outwardly directed and all very gently curved upwards on the same side of the horizontal plane. Near and at the ring the walls of the rays are fused, to give a thickened calcareous structure, and the hollow interiors of the rays communicate each by a single pore with the main central cavity.

HORIZON. Upper Jurassic and bottom Cretaceous of Europe : Lower Cretaceous of the Middle East.

MATERIAL. Numerous random thin-sections. In Iraq seen in the Sarmord Formation (Valanginian-Hauterivian) of Jebel Gara, Mosul Liwa, and Surdash, Sulemania Liwa ; from the Garagu Formation (Valanginian) of Kirkuk well no. 116 (subsurface), of Banik (Mosul Liwa) and of Fallujah Well (subsurface : Dulaim Liwa), from the Qamchuqa Formation (Barremian-Aptian) of Kirkuk well no. 116 (subsurface) and from Zibar-Isumeran (Mosul Liwa). In the Hadhramaut (Southern Arabia), seen in Barremian-Aptian *Orbitolina*-limestone from Mintaq, Wady Hajar, and from the Aptian of Ghabar.

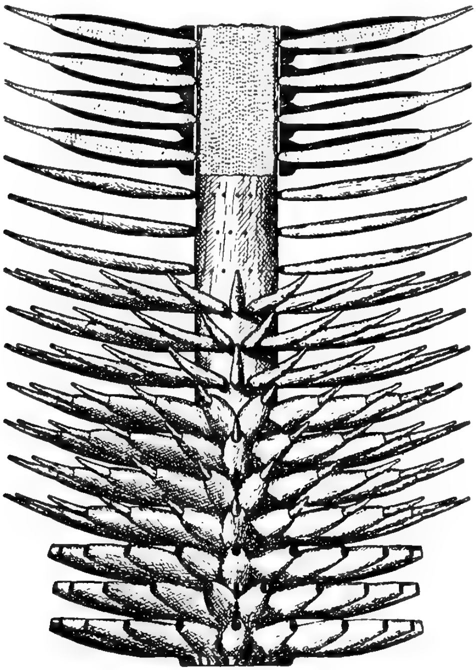


FIG. 2. Reconstruction (after Pia 1920) of *Actinoporella podolica* Alth. From top to bottom (1) vertical section (2) decalcified portion with anterior branches removed (3) decalcified portion with all branches in position (4) branches with calcareous coating in position (5) calcareous skeleton alone. ×40 approx.

REMARKS. This species, mostly Upper Jurassic in Europe, appears to be Lower Cretaceous in its Middle East occurrences. Pia, dealing with the Podolian type material, relegated *A. gümbeli* to the synonymy of *A. podolica*, regarding the differences as not significant. Carozzi referred his Swiss material to *A. podolica* likewise. This practice is now followed with the Middle East material. This latter suggests smaller verticils and possibly a lower average number of rays than in the

European fossils, but good series of solid verticils free from matrix would be needed to evaluate this decisively. Nothing like the distinctive *A. sulcata* Alth (Pia 1920 : 100, fig. 20) has been seen.

Actinoporella podolica is highly distinctive in random thin-section. Its thin-walled but coherent fragments cannot easily be confused with any species of *Clypeina*, whose verticils are more massive, except perhaps the Valanginian *C. marteli* Emberger, which has only about half the number of rays or branches per verticil. *Munieria*, apparently more solid, is much more fragmentary, and shows as smaller, more problematic debris : possibly its calcium carbonate was initially more fragile.

Genus *ANTHRACOPORELLA* Pia

DIAGNOSIS. Calcified unsegmented branched cylindrical dasyclad with close-set, aspondyl dichotomous side-branches.

Anthracoporella, described by Pia (1920), is a primitive dasyclad from the late Palaeozoic. The tubular thallus is exceptional in branching, often at a wide angle. The stem-cell is proportionally large in diameter to the surrounding wall-thickness in which the aspondyl dichotomous side-branches are very numerous, fine and closely set. The calcification may not have reached quite to the stem-cell, and the lateral branches probably projected considerably beyond the calcified zone.

In a later paper Pia (1937) listed occurrences of the type-species *A. spectabilis*, initially described from the Upper Carboniferous of the Austrian Southern Alps. Species of the genus are characteristic of the Upper Carboniferous and Permian of Alpine Europe and Asia, and occur also in the southwestern United States and in Madagascar.

In the revision of the Middle Eastern material for this study two species are recognized, the distinction being based mostly on size. *A. spectabilis* Pia is much the larger, with outer tube-diameters commonly up to 5 mm. or more (5·8 mm. quoted by Pia as a maximum ; Bebout and Coogan (1964) record up to 8·9 mm.). Smaller individuals or branches of this species, associated with the larger, may measure as little in diameter as 1·5 mm., but are exceptional. The second species, now described as new, is represented by solitary occurrences of tubes of diameter of less than 1 mm. This was at first considered a dwarfed variety and later in time than the large type-species, but their ranges overlap, and they seem distinct.

Anthracoporella spectabilis Pia
(Pl. 2, figs. 1, 2)

1920 *Anthracoporella spectabilis* Pia : 15, fig. 3, pl. 1, figs. 7–11.
1937 *A. spectabilis* Pia ; Pia : 795, 809, 822.
1960 *A. spectabilis* Pia ; Elliott : 219.

DESCRIPTION. Thallus of branched tubular dasyclad pattern, up to 5–6 mm. or more in external diameter, stem-cell cavity large, d/D ratio 50–80%, the larger examples being progressively thinner-walled. Side-branches simple, about 0·040 mm. diameter, sometimes dichotomous, aspondyl in arrangement, crowded and very

numerous, more or less at right angles to main axis and giving a characteristic dot and dash appearance in slightly oblique transverse cuts. About 20 of these radial pores seen in 1 mm. of wall in a large example, and a small example of 1 mm. diameter showed a total of about 60 (both in transverse section).

HORIZON. Both Middle East occurrences of this species are in derived material, at Jebel Busyah and Jebel Hagab, Oman, Arabia. The former occurrence is in cobbles of derived limestone in a presumed Triassic conglomerate : associated with *Anthracoporella* are the algae *Tubiphytes* and *Pseudoepimastopora*, and the limestone of a similar cobble was dated by Dr. M. Chatton as Middle Permian on the evidence of *Parafusulina shiptoni* and other foraminifera, the fusulinid being compared with that from post-Artinskian Permian somewhat younger than the zone of *P. kattaensis* of the Salt Range (M. Permian of India). The Jebel Hagab occurrence is in derived material associated with the Mesozoic Musandam Limestone. *Tubiphytes* occurs with *A. spectabilis*, somewhat recrystallized, and this appears to be derived Permian material too.

MATERIAL. See under Horizon.

REMARKS. Pia's Austrian type material was from the Upper Carboniferous-Lower Permian level ; Maslov (1956) records it from the Upper Carboniferous of the Urals, U.S.S.R. Bebout & Coogan (1964) record a large and proportionally very thin-walled form of the species from the subsurface early Permian (Wolfcampian) of Texas. Other records are discussed below under *A. mercurii* sp. nov.

Anthracoporella mercurii sp. nov.

(Pl. 1, fig. 8)

DESCRIPTION. Similar in form, growth and branches to *A. spectabilis*, but much smaller, diameter 0·5–0·9 mm. ; (relatively thicker-walled, d/D 40–60% ; pores radial (branches of 0·026 mm. diameter) ; a transverse section of one individual showed about 40 such branches).

HORIZON. Permian of the Middle East and Tunisia (see below).

HOLOTYPE. The specimen figured in Pl. 1, fig. 8 from the Permian, Bih Dolomite, of Wady Bih, Jebel Qamar, Oman. V. 52035. This limestone is dated in fusulinid evidence by Dr. Chatton as belonging to the " Neoschwagerina–Verbeekina zone of low Guadalupian age (Wordian) ".

OTHER MATERIAL. Random sections from the lower Permian of Ora and Harur, Mosul Liwa, N. Iraq (Zinnar Limestone (Artinskian) of Hudson, 1958) ; from the Permian of Jebel Qamar, Jebel Hagab, and Tawi Silaim, all Oman ; in derived Permian material in the Upper Cretaceous Hawasina formation of Juweiza Well, Trucial Oman ; and in derived Permian material associated with the Mesozoic Musandam Limestone at Jebel Hagab, Oman.

REMARKS. *A. mercurii*, while much smaller than *A. spectabilis* is distinctly larger than the tiny (Upper Carboniferous) *A. kasachiensis* (Maslov 1956), and differs noticeably in proportions of the component structures. It differs in its occasionally

divided branch-structure from the Japanese Lower Carboniferous *Anatolipora* (Konishi 1956), and similarly from the English Lower Carboniferous *Nanopora anglica* (Wood 1964) ; Wood refers *Anthracoporella fragilissima* to this latter genus also. Johnson's U.S.A. records of *Anthracoporella* from the Permian of New Mexico and Upper Permian of Texas (Johnson 1942 ; 1951) may well be of *A. mercurii*. Outside the Middle East, it occurs in the Upper Permian of Tebaga Well, S. Tunisia.

The species appears to be more wide-spread in scattered occurrences than the large localized *A. spectabilis*, and is dedicated to the god Mercury who presided over travel.

Anthracoporella magnipora Endo

1951 *Anthracoporella magnipora* Endo : 124, pl. 10, figs. 4, 5.
1963 *A. magnipora* Endo ; Flügel : 85, pl. 1, fig. 1.

This species, originally described from the Japanese Permian, is known to me in the Middle East only from Flügel's record quoted above : Permian of the Ala Dag, Taurus Mountains, Southern Turkey.

Genus ***ATRACTYLIOPSIS*** Pia 1937

Diagnosis. Fusiform, cylindrical or ovoid tubes formed of adjacent touching or fused hollow calcified spheres.

Atractyliopsis was proposed by Pia (1937) for certain Upper Palaeozoic algal microfossils which consist essentially of groups of adjacent, touching or fused hollow calcified spheres, occurring in the form of fusiform, cylindrical or bead-like bodies. These were regarded by him as somewhat similar to his earlier genera from the Triassic, *Aciculella* and *Holosporella* (Pia 1930). These he had interpreted as the remains of dasyclads in which the only calcified structures were the walls of endosporic sporangia set subperipherally within the main stem-cell, and he compared these with the Triassic *Diplopora phanerospora* in which these structures are seen within a normal calcified diplopore wall-structure. *Holosporella* is a hollow tube ; *Aciculella* a solid shaft, regarded as calcified internally during the lifetime of the alga.

Pia gave three figures of *Atractyliopsis*, two Carboniferous, one Permian, without assigning a type-species or species-names ; he considered these fossils as fusiform segments. The Permian form was later named *A. lastensis* (Accordi 1955), fully described from Italian topotype material, and recognized as cylindrical in form. Meanwhile Wood (1940) described the similar *Coelosporella* from the English Carboniferous, and mentioned its cylindrical form as differing from the alleged fusiform *Atractyliopsis*. *Coelosporella* however shows a much more solid wall than the other forms, and ovoid outwardly-directed sporangia, and may be regarded as valid on these grounds. *Atractyliopsis*, which differs only in larger dimensions and geological age from the earlier-described *Holosporella*, is retained here, since such fossils could originate from dasyclads of very different pattern.

In the Middle East only one species of *Atractyliopsis* is known : this occurs in a somewhat similar facies and at the same level as the type-species, but less abundantly.

Atractyliopsis darariensis sp. nov.

(Pl. 2, figs. 3, 4, 5)

1960 *A. lastensis* Accordi ; Elliott : 219.

DESCRIPTION. Hollow cylindrical tubular structures, straight or gently curved, of up to 5·0 mm. observed length, 0·73 maximum external diameter : walls formed of a single layer of adjacent, touching or fused hollow spheres of 0·13 mm. internal diameter, original wall-thickness of spheres variable but 0·010–0·020 mm. in detached spheres. Primary calcification variable : the spheres may be more or less set in calcite formed by their fused walls, or almost isolated, with the outer surface of the cylinder truncating their outer curves, sometimes completely, to leave external openings, and their inner curves projecting roundly and unabraded into the cylinder-cavity.

HORIZON. Upper Permian of Northern Iraq.

HOLOTYPE. The specimen figured in Pl. 2, fig. 5, from the Upper Permian Darari or Upper Chia Zairi Formation, Ora, Mosul Liwa, North Iraq ; V. 52037.

PARATYPES. The specimens figured in Pl. 2, figs. 3, 4, same horizon and locality as the holotype ; V. 52015, 52037.

OTHER MATERIAL. Fragments in random thin-sections, same horizon and locality.

REMARKS. This is very closely related to the type-species *A. lastensis* Accordi from the Upper Permian Dolomites of Northern Italy (Accordi 1956). Both occur with a similar *Gymnocodium*-flora in a rather similar facies at the same level. *A. darariensis* is described here as distinct since the cylindrical remains seem to have been markedly longer than in the Italian species, but the two are probably contemporary geographical species at most. Much depends on secondary calcification, which has to be distinguished very carefully where possible from that of the original sporangial coatings, and the Italian and Iraqi specimens are differently preserved in this respect. The measurements given above under " Description " are carefully taken from specimens without secondary calcification, or with it easily distinguishable as such when present. In the Italian topotype material available to me *Atractyliopsis lastensis* is much more abundant than in the Iraqi material, where *A. darariensis* is a minority-constituent in a flora of *Gymnocodium* and *Permocalculus*.

The Iraqi species is distinct from the Austrian *A. carnica* E. Flügel. Although described in great detail (E. Flügel 1966), the abundant material figured and described by this writer shows only circular and oval cross-sections.

Praturlon (1963a : 132) has figured a thin section which shows *Atractyliopsis* set vertically (axially) within *Permocalculus* cf. *forcepinus* (Johnson), (Chaetangiaceae or perhaps Codiaceae). He makes the interesting suggestion that this is the asexual form of the species, which is associated with other specimens of *Permocalculus* showing normal " sporangia " (?cystocarps) and regarded as the sexual form. That is, the *Atractyliopsis* is to be regarded as part of the internal structure of the *Permocalculus*, and is therefore not a dasyclad, nor indeed, a separate alga at all.

In the Iraqi material *Atractyliopsis* is associated with very abundant *Permocalculus*, but is itself rare. It is confined to the Darari Formation or top division of the Iraqi Permian, whereas *Permocalculus* ranges through the whole Chia Zairi, representing most of the system. It has never been seen inside *Permocalculus* in this material in the present study. The occasional occurrence of smaller fossils within larger ones by normal disturbance of randomly associated material on the sea-floor is not uncommon (cf. the perfect fit of the Palaeocene codiacid *Ovulites* within the dasyclad *Trinocladus* ; Pl. 23, fig. 2). With this in mind, I prefer to retain the older view of Pia (1937), that *Atractyliopsis* represents a zone of calcified sporangial structures set marginally in the dasyclad stem-cell. There is no direct proof of this for *Atractyliopsis* itself, but a comparable structure exists in *Diplopora phanerospora* Pia (Pia 1926), where both internal and external structures are calcified and the morphology is such that accidental post-mortem fitting is impossible.

Genus ***BELZUNGIA*** Morellet 1908

DIAGNOSIS. Hollow ovoid or elongate bead-like calcareous units, open at both ends : the thick wall perforated by verticils of radial dichotomising and swollen canals, which terminate externally as a pattern of small pores.

Belzungia (Morellet 1908) bears the same relation to *Thyrsoporella* as *Cymopolia* does to normal tubular dasyclads : that is, it possesses similar verticil-structure, but is organized into separate units or bodies, united in life into a jointed branching thallus, rather than the standard dasyclad single skeletal tube. *Belzungia* and *Thyrsoporella* are in fact identical in the plan of their peculiar lateral branch-structure within the calcareous wall-thickness.

In the Middle East *Thyrsoporella silvestrii* Pfender is a common Eocene fossil. Rarely, there occur isolated examples whose external morphology suggests reference to *Belzungia*. The best example seen of this was a specimen, from the Middle Eocene Pila Spi Limestone of Koi Sanjak, Erbil Liwa, Northeast Iraq. The dimensions are however those of a *Thyrsoporella* rather than of the larger *Belzungia*. L. Morellet, in an unpublished pioneer report of January 1931, compared a similar specimen from the Palaeocene of the Sulemania district (N.E. Iraq) to the smaller of the French Eocene species, *B. terquemi* Morellet, but the enlargement on the micrographs given him was inaccurate, and measurement of the actual specimen shows that it was smaller.

NOTE. Part 2 of Massieux (1966b), in which this author compares *Thyrsoporella* and *Belzungia* in detail, and refers *T. silvestrii* to *Belzungia*, was seen too late for proper discussion in this work. However, the specimens studied in the present work show the heavily-calcified walls of *Belzungia*, but the branch-system appears like that of *Thyrsoporella*.

Genus ***BROECKELLA*** L. & J. Morellet 1922

DIAGNOSIS (after Morellet). Hollow calcareous units, keg-shaped, traversed along the axis by a tube open at the extremities. Annular cavity between the outer walls

and tube-walls, divided by horizontal floors into successive compartments, each of these itself divided by radial septa into several chambers each communicating by a single pore with the axial tube, and by numerous pores with the exterior, riddling the outer wall. Pores opening in the axial tube set in regular verticils ; external pores set in irregular sinuous lines.

Broeckella is a peculiar dasyclad described by Morellet (1922) from the Belgian Montian, and subsequently recognized from about the same level in Austria and Cuba (Keijzer 1945). These occurrences are of the type-species, *B. belgica* Morellet : *B. ranikotensis* (Walton) is known from the Indian Palaeocene (Walton 1925 ; Pia 1928), and the little *B. minuta* Carozzi from Switzerland is presumed Palaeocene.

Broeckella as described by Morellet (1922) is an extinct dasyclad whose skeletal remains occur as little keg- or short barrel-shaped units. Each unit contains a fairly wide central canal extending vertically from end to end, which once housed the main stem-cell of the plant. The apparently thick structure between outer surface and inner central canal is hollow, being divided by thin horizontal platforms into annular cavities, which are themselves divided into segment-shaped chambers by thin radial vertical walls. Each of these chambers (primary branches) communicates with the exterior by numerous small pores in the outer wall, said to open in sinuous lines, and with the interior canal by one large pore each, through the inner wall, arranged in horizontal rings. The distinctive thin-section appearance has been very well figured by Keijzer (1945). The numerous relatively large interior cavities between inner and outer walls have irregular surfaces to septa and partitions, made still more so by secondary calcification, and random cuts give curious irregular-radial patterns not like those of more conventional dasyclads such as *Cymopolia*, where there is a greater proportion of wall-material to original cavity in life.

The wide but scattered Tethyan distribution of this genus, its probable ancestry and its restricted geological range have been discussed (Elliott 1962b) ; I concluded that it was a primitive genus occurring uncommonly even under optimum algal conditions in the Palaeocene, and then becoming extinct.

Broeckella belgica L. & J. Morellet

(Pl. 3, fig. 1)

1922 *Broeckella belgica* Morellet : 22, pl. 2, figs. 56, 57.
1945 *Broeckella belgica* Morellet ; Keijzer : 178, pl. 6, figs. 84–86.
1960 *Broeckella belgica* Morellet ; Elliott : 225.
1962 *Broeckella belgica* Morellet ; Elliott : 51.

DESCRIPTIONS. The characters of this, the type-species, are those of the genus. The Middle Eastern material consists of random thin-sections only, similar to Keijzer's Cuban material. Of described species, the Indian *B. ranikotensis* (Walton) is the largest, and the Swiss *B. minuta* the smallest : the Belgian Cuban and Middle East specimens are all referred to *B. belgica* Morellet. Some dimensions for comparison are listed below.

Measurements and detail of ***Broeckella*** spp. Dimensions in mm.

	belgica (type)	*belgica* (Cuba)	*belgica* (M.E.)	*ranikotensis*	*minuta*
Length of unit	1·3	up to 2·0	1·04	3·5–5·0	0·45–0·90
Outer diam. of unit	1·8	1·4–2·5	1·10	2·0–2·5 (max)	0·25–0·45
Central canal diameter	0·6	0·35–0·8	0·4	0·66–0·83 (max)	0·05–0·15
No. of verticils per unit	4	4–6	4	20 approx.	numerous units (fused)
No. of primary branches per verticil	8–12	10–15	12 appr.	15–20	15–20

HORIZON. Palaeocene of Europe, Cuba and Middle East.

MATERIAL. Random thin sections from the Palaeocene Sinjar Limestone of Kashti, Sulemania Liwa, North-east Iraq, and from the Palaeocene of Sahil Maleh, Batinah Coast, Oman, Arabia.

REMARKS. Both these occurrences are in rocks yielding a varied and characteristic Palaeocene algal microflora, as well as typical foraminifera for this level.

Genus *CLYPEINA* Michelin 1845

DIAGNOSIS. Flat, saucer-, bowl- or funnel-shaped calcareous discs formed of horizontally-fused radial tubes : centrally they meet in a stout calcareous ring, each tube communicating by a single pore with the central cavity : the central ring is thickened below by the fused bases of the radial tubes and sometimes a smaller similar feature shows on the upper surface. In life these were the calcified structures of fertile dasyclad whorls.

Clypeina occurs as small fossil calcareous discs, saucer-, bowl- or funnel-shaped, centrally perforate, and with the solid portion composed of fused radiating tubules : communicating each by a single core with the central cavity. Usually the discs are separate, but occasionally several occur together in vertical, consecutive association. Described by Michelin (1845 : 177) from the French Oligocene as a coral, it was subsequently referred to other marine invertebrate groups by various authors until Munier-Chalmas (1877), in a brief communication, drew attention to its true algal nature.

Clypeina was reconstructed from Eocene material to show the probable structure and appearance of the plant in life (Morellet & Morellet 1918). These authors showed a dasyclad with central stem-cell bearing whorls of thin hair-like sterile branches below, and fused calcified cuplike fertile whorls above, each fertile whorl partially embracing the next : the plant is completed by a tuft of hair-like branches forming the terminal umbel, calcified at the base to give a perforate, " pepper-pot top ", structure (Fig. 3). The Morellets worked on loose, dissociated, elements from the unconsolidated sediments of the Paris Basin, and besides typical fertile whorls

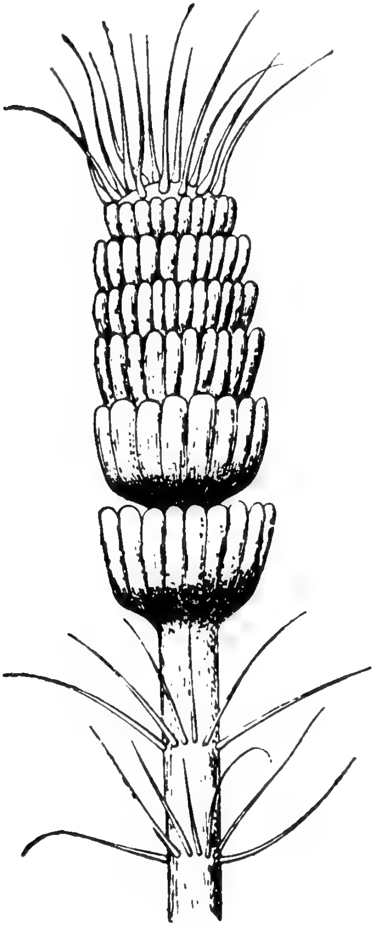


FIG. 3. Reconstruction (after Morellet 1918) of *Clypeina*. Sterile whorls below, fertile (calcified) whorls above, terminal tuft at top. ×30 approx.

they had calcified evidence of the sterile portion of the plant, of the lower, atypical fertile whorls, of the terminal structure, and of the serial association of the fertile whorls.

Pia (1927) placed *Clypeina* in the tribe Diploporeae, and he was followed in this attribution by Emberger (1944) and Kamptner (1958). The Morellets (1913 : 31 ; 1918 : 102), students of Tertiary and Recent algae, grouped *Clypeina* under Acetabulariae with *Halicoryne*, *Acetabularia* and *Acicularia*, three genera still surviving, and all showing separate sterile and fertile whorls and of somewhat similar morphology. Rezak (1957) summarizing this, agreed with the Morellets in their attribution. *Clypeina* is now placed in a new tribe Clypeineae, for its geological appearance

precedes the evolution of the choristospore structures with which the terminal discs of Acetabulariae have been thought homologous. It therefore seems probable that it represents an earlier development of similar morphology, but from a different source. This point is more fully discussed below under dasyclad evolution (p. 99).

In the Middle East *Clypeina* is represented by species in the Upper Jurassic and basal Cretaceous, and again in the older Tertiary (Palaeocene and Eocene). A clypeiniform alga, still incompletely known, occurs in the Permian, and a Triassic species is now known from elsewhere (Pantić 1965). The numerous species listed throughout the Cretaceous succession in the western Mediterranean area (Algeria, France, etc.) by Emberger (1957) have not been noted in Middle Eastern material during the examination of thousands of thin-sections, often richly algal, and in fact only three records occur for this portion of the geological column.

Clypeina jurassica Favre

(Pl. 3, figs. 2–5 ; Pl. 4, figs. 4, 5, 6)

1927 *Clypeina jurassica* Favre : 34, pl. 1, figs. 2, 3 ; text-figs. 10, 11.
1932 *Clypeina jurassica* Favre ; J. Favre : 12, text-fig. 2.
1951 *Clypeina jurassica* Favre ; J. Morellet : 399, pl. 22.
1955b *Clypeina jurassica* Favre and *C. hanabatensis* Yabe & Toyama ; Elliott : 125.
1958a *Clypeina jurassica* Favre ; Donze : 21.
1962 *Clypeina jurassica* Favre ; Powers : 131.

Description (from Middle Eastern material). Discs (fertile verticils), saucer to open-funnel shaped, diameter up to 2·4 mm., height up to 0·75 mm. composed of up to 24 fused radiating tubules (sporangial elements) around a central cavity of up to 0·5 mm. ; the majority of normal specimens are about 2·0 mm. diameter, with 18–20 tubules and central cavity of about 0·4 mm. The tubules widen slowly outwards, and the outer ends are open : on the external surfaces, upper and lower, the tubules are demarcated by shallow grooves. Although in normal specimens the tubules are nearly circular in cross-section, they tend to vary according to the size of the disc of which they form part, and in the larger examples, with more numerous tubules, the tubule cross-section shows the height greater than the diameter. The tubules fuse to form a conspicuous thickened central basal ring on the lower surface of the disc : this is most developed in the funnel-shaped examples. In a large example of estimated 2·5 mm. disc-diameter or more, the inner diameter of a single tubule increases from 0·130 mm. near the centre to 0·390 mm. in 1 mm. tubule-length : the diameter of the single inner communicating pore between central cavity (stem-cell) and tubule is 0·050 mm. ; and the single wall-thickness about the middle of the tubule is 0·065 mm. In random thin-section the united walls, back to back, of any two adjacent tubules show as radial fibrous calcite, clear or yellow, separated by a dark line, and in horizontal (transverse) sections these median structures project radially at the margin, to give a torn serrated appearance to the whole disc. This wall-structure and the open ends of the tubules, whatever their significance in terms of the original plant-calcification or subsequent diagenesis, are characteristic of the

species, whether preserved in limestone or marl, and there is normally no confusion with the Valanginian species *C. lucasi* Emberger.

HORIZON. Upper Jurassic ; circum-Mediterranean and Middle East.

MATERIAL. Numerous solid and thin-section specimens from Qatar Peninsula, Persian Gulf, where it is abundant in the subsurface Upper Jurassic " Arab Zone " (Fahahil and Qatar Formations : Sugden *in press*) probably of Kimmeridgian-Tithonian age. Also at the same level in north-eastern Saudi Arabia (Powers 1962), and in Gezira no. 1 well, Murban, Abu Dhabi, Trucial Oman. Associated microfossils are the alga *Salpingoporella annulata* Carozzi and the microcoprolite *Favreina salevensis* (Paréjas). Thin-section material from both Kirkuk and Samawa, Iraq, where it abounds likewise in the subsurface Najmah Formation, of about the same age, with the same companions. Also seen in thin-sections from the topmost Jurassic at Haushi, Southern Oman, Arabia, accompanied by debris probably referable to *Griphoporella perforatissima* Carozzi, an alga initially described from the Upper Portlandian and Berriasian of Switzerland. The species is common in the Upper Jurassic of numerous exposures in southern Persia (Gollestaneh Coll.).

REMARKS. *Clypeina jurassica* is a common microfossil in the Upper Jurassic of southern and central Europe, North Africa and the Middle East, and records of it are very numerous. Described by Favre (Favre & Richard 1927) on thin-section material from Switzerland, and re-described for comparison with *Clypeina inopinata* (Favre 1932), the next advance was the description of Algerian material by Morellet (1951) based on both thin-section and solid (silicified) specimens. Donze (1958a) re-described material from the type-area from a good selection of solid specimens, presumably isolated by weathering or artificial breakdown of weathered material. For the present study of Middle East examples both numerous thin-sections and solid examples obtained by washing of crumbled core-material have been available.

The descriptions drawn up for this species by Favre, Morellet, Donze and myself all differ slightly in detail. The principal difference is that specimens from the type-area (Switzerland) show a lesser maximum number of sporangial tubules per verticil than do those from some other localities. For Swiss material Favre gives a relevant count of 10–17, and Donze 7–17, whereas Morellet, with Algerian examples, gives 11–20, and the Middle East material (above), shows up to 24. Although there are numerous figures in the literature of random cuts of this species conforming in this particular with the type-material, there are some which indicate a higher count (e.g. de Castro 1962, pl. 18 ; Italy, Naples area). These higher counts are from more southern areas than that of the type-material. It would seem that this is a case where the historical development of western Europe has resulted in the original description of Tethyan material being made in a marginal area, a phenomenon familiar both in stratigraphy and palaeontology.

Other differences observed in the Qatar (Middle East) specimens were the somewhat variable convexity of the verticils, and the prominence of the central thickened ring on the lower verticil surfaces. The former was however recorded by Donze on topotype material, and indeed is to be expected from our understanding of the growth

of the living *Acetabularia*. The latter character was described by Morellet, but not well figured, on Algerian material.

The pioneer study on Middle East (Qatar) material was by F. R. S. Henson in an unpublished report of 1942. He distinguished a minority of *C. jurassica* conforming strictly with the type-description, and more numerous examples with a higher sporangial-tubule count. In a preliminary examination of Middle East algae (Elliott 1955b) I recorded these latter as *C.* cf. *hanabatensis* Yabe & Toyama, comparing them with this Japanese species which has a higher count (22–24, up to 27), but is a larger species (verticil-diameter up to 3·5–4·0 mm.). This determination is now abandoned.

Detailed comparative statistical studies of local populations of *Clypeina jurassica* from different circum-Mediterranean and Middle East countries have not been made to my knowledge. Such studies would have to be made on good collections of complete, isolated, verticils, since the recognition of proportional, as opposed to structural, differences, in random thin-section material is a task of great difficulty, at any rate with the small degree of difference expected in the present problem. The results would have to be interpreted in the light both of presumed salinity changes, from facies and accompanying fauna, a factor affecting living algae, and also bearing in mind possible post-mortem sorting of verticils of slightly differing size and shape from mixed assemblages of dissociated component-verticils derived from associated plants. It seems likely that the local differences revealed, at any rate in the main Tethyan basin, would depend on these secondary factors rather than on a progressive evolutionary trend.

C. jurassica is a frequent and characteristic fossil for much of the Upper Jurassic of the western old-world Tethys ; in the east, it is missing from rocks of this age in Borneo. The oldest level appears to be in Algeria (Rauracian-Sequanian of Morellet 1951, equalling Upper Oxfordian of current usage) ; the species occurs throughout the Mediterranean Kimmeridgian and is especially abundant at levels of Portlandian or Tithonian age over the whole of its distribution-area. In my experience it extends to the very top of the Upper Jurassic and is a good index-fossil for the upper part of the Upper Jurassic. (See also comments below (p. 87) on the Jurassic-Cretaceous boundary.)

In the Franco-Swiss area, from which the types were described, there are records from the lowest Cretaceous (infra-Valanginian and Berriasian, e.g. Donze 1958a, b). This is in an area adjacent to a region of uplift with terminal Jurassic—early Cretaceous freshwater brackish and lagoonal beds of Purbeck type : the algae are consistently smaller than those from the Jurassic. They may be a transitional form to the succeeding *C. inopinata* (rare or absent in the Middle East), their evolution a reaction to salinity-changes. Donze suggested, that they were either a different species, close to *C. inopinata*, or stunted *C. jurassica* " bad adaption to environment ". The relation of these and other algae to salinity is discussed below under environment. In Jugoslavia Kercmar (1962) has described a local variety *C. jurassica minor*, which he distinguishes from the typical *C. jurassica jurassica* mostly by the smaller size, there being little if any overlap or transition in this character.

He regards this small variety as possibly transitional to *C. parvula*. It certainly seems that *C. jurassica* was the rootstock for other and later species, and that this evolution may well have been connected with areas of late-Jurassic uplift and emergence.

Clypeina inopinata Favre 1932

This species, described by Favre (1932) as distinct from *C. jurassica* and as succeeding it in the Swiss Valanginian, is not known to me with certainty from the Middle East, although basal Cretaceous is well-represented in available collections. Occasional qualified records in unpublished reports are based on rare and fragmentary *Clypeina* sp., and no good *C. inopinata* have been noted. The species may be a local successor to *C. jurassica* in the Franco-Swiss area only. M. Dufaure of Bordeaux informed me (personal communication 1965) that the type-occurrence of *C. inopinata* is, in fact, Upper Berriasian i.e. pre-Valanginian.

Clypeina lucasi Emberger
(Pl. 5, fig. 4)

1956 *Clypeina lucasi* Emberger : 549, pl. 24, f. 1, 2, 7.
1960 *Clypeina lucasi* Emberger ; Elliott : 223.

DESCRIPTION (after Emberger). Fertile verticils almost flat, circular, diameter 2·5–3·0 mm. and about 0·5 mm. thick : 12–18 club-shaped sporangial chambers, of about 1·1 mm. long and max. diameter 0·5 mm., fused laterally for $\frac{3}{4}$ of their length, separated by shallow grooves, and terminally imperforate. Central cavity of 0·35–0·48 mm. diameter, margined by a feeble raised ring above and a more prominent one below.

HORIZON. Valanginian of Algeria and Oman.

MATERIAL. Thin-sections in basal Cretaceous limestones (Thamama Formation Equivalent), Hugf area, southern Oman, Arabia.

REMARKS. This distinctive species was described by Emberger (1956) from solid (silicified) specimens found in the Algerian Valanginian, where it was accompanied by *Clypeina marteli* Emberger, also new. In the Middle East the two species occur, together with the codiacid *Arabicodium aegagrapiloides* Elliott, at the same level in Southern Oman, Arabia. In the thin-sections of limestone *C. lucasi* may be recognized, the details corresponding with much of Emberger's description.

Clypeina marteli Emberger
(Pl. 4, fig. 1)

1956 *Clypeina marteli* Emberger : 550, pl. 24, f. 3–6.
1960 *Clypeina marteli* Emberger ; Elliott : 223.

DESCRIPTION. Stellate verticils, gently curved, diameter 1–2 mm., consisting of from 7 to 12 radiating tubules, fused laterally for about the inner third of their length and then free outwards, surrounding an inner circular cavity of from 10–14% of the

verticil diameter. Tubules circular in cross-section, terminally bluntly rounded, thin-walled (wall-thickness 0·026 mm. in a tubule of outer diameter 0·130 mm. ; verticil-diameter 1·5 mm. approx.), and forming a moderately developed raised central ring below, but without similar feature above : the tubules communicate with the central cavity each by a single pore.

HORIZON. Valanginian of Algeria and Oman.

MATERIAL. Found in the basal Cretaceous (Lower Thamama equivalent) of Hugf, Southern Oman, Arabia, i.e. at about the same horizon as the type-level in the Algerian Valanginian, and similarly associated with *Clypeina lucasi* Emberger, and also with the codiacid *Arabicodium aegagrapiloides* Elliott.

REMARKS. *Clypeina marteli* is highly distinctive amongst species of its genus : the only other stellate species in which the radiating tubules are similarly free for much of their length are *Clypeina digitata* (Parker & Jones) Morellet emend. Rezak, and (less closely comparable) *C. helvetica* Morellet, both Eocene. Emberger's comparison with the former drew attention to the gently concave plane of *C. marteli* as compared to the more funnel-shaped form of *C. digitata*, a valid distinction (Emberger 1956). *C. marteli*, however, does show a central fusion ring, marginal to the stell-cell cavity, on its lower surface, though this is regular in form and not irregular as that of *C. digitata* described by the Morellets (1913).

More serious risk of confusion exists with *Actinoporella podolica* Alth, which similarly occurs at about Valanginian level in the Middle East. However, although both are somewhat similar in size, *Actinoporella* shows many more tubules per verticil (18–20 as opposed to 7–12, and the former smaller in size), and a proportionally larger central cavity (d/D 20% or more, as opposed to 10–14% in *C. marteli*).

Clypeina parvula Carozzi
(Pl. 5, figs. 5, 6)

1946 *Clypeina parvula* Carozzi : 24, fig. 1.
1948 *Clypeina parvula* Carozzi ; Carozzi : 355, figs. 50, 51.
1955b *Clypeina parvula* Carozzi ; Elliott : 126.
1960 *Clypeina parvula* Carozzi ; Elliott : 222, 223.

DESCRIPTION (after Carozzi). Sterile whorls in the form of straight thick-walled calcareous tubes, widening in the upper portion and with the outer surface showing a number of shallow straight vertical flutings or concavities, usually about twelve, but from ten to twenty-five recorded. The fertile whorls are similar but widen much more, terminating in a kind of peripheral fringe or collar : internally, sporangial chambers correspond to the external flutings, the actual cavities being set in the thick calcareous wall. External diameter is said to be from 0·09–0·45 mm. and the diameter of the central canal 0·03–0·12 mm. (average 0·07 mm.).

HORIZON. Upper Jurassic—bottom Cretaceous Europe (?Aptian–Albian Jugoslavia, see Radoičić 1960), bottom Cretaceous Middle East.

MATERIAL. In Iraq, from the lower part of the Cretaceous (about Valanginian

level) : Sarmord Formation of Jebel Gara and Garagu Formation of Banik (both Mosul Liwa) ; also subsurface Garagu at Kirkuk.

It has also been seen in the bottom Cretaceous at Haushi, Southern Oman, Arabia, where it was accompanied by the dasyclads *Acicularia*, *Salpingoporella*, and *Griphoporella*, also by *Permocalculus* : the level was independently dated by foraminifera.

REMARKS. The details given above are summarized from Carozzi's descriptions. His reconstruction shows a somewhat peculiar little alga, consisting of inverted fluted cones inserted within one another vertically. His thin-sections substantiate the detail quoted above and also show further detail. This species, if correctly interpreted as a *Clypeina*, departs more from the usual verticil-morphology than other species. In the Swiss Purbeckian (terminal Jurassic) *C. parvula* occurs in beds interpreted as freshwater, its companion fossils being charophytes and ostracods.

In the bottom Cretaceous, marine Valanginian level, of the Middle East there occur not uncommonly in thin-section preparations sections corresponding mostly to the transverse cuts of the bases of verticils as figured by Carozzi. Occasionally vertical cuts are seen, but never the transverse cuts he figures of the upper portions of fertile verticils, which show the sporangial cavities, outer collar, and other detail. The number of flutings is usually from 8 to 10, and the size-range falls for the most part in that quoted above from Carozzi, though one large example had an external diameter of 0·6 mm.

These little fossils, with occasional charophytes and ostracods, occur in Iraq to form a subordinate element in a rich marine dasyclad and other algal flora, which includes species of *Actinoporella*, *Cylindroporella*, *Salpingoporella*, *Permocalculus*, *Lithocodium* etc., also foraminifera and microproblematica, marine mollusca and corals. They are interpreted as *Clypeina parvula* from coastal freshwater beds, which, together with the charophytes, have been washed out to sea before burial. Only the more resistant parts of the verticils survived this derivation, which would explain the absence of the more fragile reproductive structures.

Clypeina spp. (Cretaceous)

1960 *Clypeina* spp. Elliott : 225.

Three records only of the genus may be made for the whole of the Cretaceous examined above the basal portion (Berriasian-Valanginian) yielding the species already described.

The specimen figured as " *Munieria baconica* Deecke " (Elliott 1958, pl. 48, fig. 1) is not of this species and may be a *Clypeina* ; it comes from the Aptian-Albian of Surdash, Sulemania Liwa, Iraq.

Another occurrence is in the Cenomanian, subsurface Mahilban Formation of Fallujah Well, Dulaim Liwa, Iraq. Fragmentary material indicated a *Clypeina* sp. of estimated whorl-diameter 3·25 mm., showing approximately 50 fused adjacent sporangial tubules of 1·04 mm. length, circular in cross-section and of 0·36 mm. near-

terminal external diameter and 0·23 mm. internal diameter. This material is insufficient for description, and it is not known if it corresponds with any of the undescribed Cenomanian species listed by Emberger (1957). The remains were associated with fine debris of codiacid algae.

A third Cretaceous *Clypeina* occurred higher, in the Maestrichtian (Shiranish Formation) of Diyana, Rowanduz Liwa, Iraq. It showed only a transverse section of sporangial tubules of about 0·13 mm. diameter. This is quite inadequate for comparison with such species as *Clypeina sahnii* Varma (1952) from the Danian of India.

Clypeina merienda Elliott

(Pl. 4, figs. 2, 3, 7, 8)

1955b *Clypeina merienda* Elliott : 127, pl. 1, figs. 8, 9.

DESCRIPTION. Fertile verticils disc-like, circular and flat, with diameter up to 2·5 mm., and diameter of central cavity up to 1·0 mm. The verticils consist of about 50 or more radiating hollow tubules, set nearly horizontally to the vertical axis, with the tubules united laterally and often slightly expanded at the periphery, where they are often open. Circular in cross-section, they have a transverse diameter of 0·15–0·18 mm. measured in the mid-zone of large examples, with internal diameter of 0·072 mm., but examples with smaller diameters than this are common and there would seem to be some variation in this character. The expanded and open tubule-ends at the periphery are variable, and may be an indication of spore-shedding in mature whorls. Internally each tubule communicates by a pore with the central cavity : fused calcification forms a thickening in this central zone and extends down to the next whorl. Up to six whorls have been seen in serial association as in life : these whorls, measured vertically in the mid-zone of the tubules, from centre to centre of consecutive whorls, were from 0·34–0·52 mm. apart.

HORIZON. Palaeocene–Lower Eocene of the Middle East.

MATERIAL. In northern Iraq, from the Sinjar Formation of Banik (Mosul Liwa), of Koi Sanjak (Erbil Liwa), and of Sirwan (Sulemania Liwa) ; also from the Kolosh Formation of Surdash (Sulemania Liwa). In southern Iraq, the species occurs in a fragmentary state in the Basita Beds of the Umm er Rudhama Formation (Palaeocene-Lr. Eocene) near Aidah, Diwaniyah Liwa.

REMARKS. This *Clypeina* is distinctive in the large number of radial tubules per whorl, in which character it somewhat resembles the larger *Orioporella* from the Belgian Montian and Indian Danian (Morellet 1922, Pia 1936b), but with no trace of the pores which perforate upper and lower surfaces of the tubules in this genus. *C. merienda* is larger than the Eocene *Clypeina* spp. described by the Morellets (1913 ; 1922) : the frequent flatness of its whorls is noticeable, though there is some variation in this character. Of Middle Eastern species, it is the one in which serially associated whorls, as in life, are most often seen in the fossils.

Clypeina sp. (Palaeocene)

(Pl. 5, fig. 2)

1960 *Clypeina.* spp. Elliott: 225.

Apart from *C. merienda*, there occur rarely in the Palaeocene-Lower Eocene of the Middle East small *Clypeina* spp. inviting comparison with those from the French Eocene described by L. and J. Morellet (1913 ; 1922 ; 1939 ; see also Rezak 1957). Random thin sections of these have been noted in material from the Palaeocene Sinjar Limestone of Banik, Mosul Liwa, northern Iraq ; from the Palaeocene Ghurna Beds (Umm er Radhama Formation) of Al Ghurra, Diwaniya Liwa, southern Iraq ; from the Palaeocene-Lower Eocene of Sahil Maleh, Batinah Coast, Oman, Arabia ; and from the Palaeocene of Aqabar Khemer, Hajar, Hadhramaut. The example figured is typical and shows a verticil of 1 mm. diameter, central aperture of 0·36 mm. diameter, with about 22 adjacent sporangial tubules. None of these localities have yielded enough material for a precise determination by comparison with the similarly-sized, well-known and beautifully-preserved European material.

?***Clypeina*** sp. (Permian)

(Pl. 5, figs. 1, 3)

1958a *Clypeina* Mich. (ou genre nouveau très voisin) Emberger : 51.
1960 ?*Clypeina* sp. Elliott : 219.
1965 *Eoclypeina* Emberger MS ; Glinzboeckel and Rabaté : pl. 74.

In a preliminary note on the Upper Permian of Djebel Tebaga, southern Tunisia, Emberger (1958a) listed a clypeiniform alga of which he proposes to describe three new species ; this has been illustrated but not described in Glinzboeckel and Rabaté (1965). Debris of the same or a similar form is now figured from the Permian of Iraqi Kurdistan, where it occurs rarely at Harur (Mosul Liwa), both from the base of the Satina Evaporite formation and from the top of the Zinnar Formation immediately below. Whether this is a true *Clypeina*, ancestral form or homoeomorph, it seems to represent an early attainment of the umbrella-like sporangial disc familiar in certain Mesozoic and Tertiary genera : it is hoped that M. Emberger's descriptions will throw light on this. The Jugoslav Permian dasyclads *Salopekiella* and *Likanella* (Milanović 1965 ; 1966) bear no close resemblance, and nothing else associated is at all comparable.

The recent description of *Clypeina besici* Pantić (1965) from the Upper Triassic of Jugoslavia is a valuable confirmatory link between the Permian *Eoclypeina* and the familiar Upper Jurassic *C. jurassica*.

Genus ***CYLINDROPORELLA*** Johnson

Diagnosis. Cylindrical calcareous bodies terminally tapered or rounded, interpreted as serial dasyclad units arranged in life somewhat similarly to those of the Recent *Cymopolia*. Internally the longitudinal central canal (stem-cell cavity) is surrounded by rings of proportionally large spherical sporangial cavities alternating

with whorls of infertile primary branch-canals. These are normally at right angles to the longitudinal axis, and each divides terminally into secondaries. Sporangia and infertile branches alternate in position in successive whorls.

Cylindroporella is a distinctive Mesozoic dasyclad first described by Johnson (1954b) : type-species *C. barnesii* from the Albian Edwards Limestone of Texas. Elliott (1957) described new species from both Upper Jurassic and Lower Cretaceous of the Middle East, and has since recognized *C. barnesii* there. The Jurassic species *C. texana* Johnson (1961a) and *C. ellenbergeri* Lebouché & Lemoine (1963), and the Upper Cretaceous *C. elassonos* (Johnson & Kaska, 1965), have not yet been identified from the Middle East.

Cylindroporella barnesii Johnson

(Pl. 6, figs. 3, 4)

1954 *Cylindroporella barnesii* Johnson : 788, pl. 93, figs. 1–7.

DESCRIPTION. The characters of this, the type-species, are those of the genus. The table below gives the various measurements by which the three species recognized in the Middle East may be distinguished.

HORIZON. Albian of Texas : Lower Cretaceous of Iraq.

MATERIAL. Fragmentary material referable to this species has now been recognized from two localities in Iraq : from the subsurface Garagu Formation (Valanginian-Hauterivian) of Makhul no. 2 well, Mosul Liwa, and from the Sarmord Formation (about Aptian level) at Sekhaniyan, Surdash, Sulemania Liwa.

REMARKS. Both the above occurrences show a *Cylindroporella* with outer diameter of 0·468 mm., inner diameter 0·156 mm., and sporangial diameter of 0·156 mm. ; they are distinct from the larger *C. sugdeni* Elliott, which they overlap in range, and seem best referred to the type-species, described from the Albian.

Detail of *Cylindroporella* spp. (M.E.). Dimensions (in mm.)

	arabica	*barnesii*	*sugdeni*
Length of segment	1·43	2·8–5·1	3·0+
Diameter of segment	0·31–0·57	0·38–0·55	0·78–1·14
Diameter of central canal	variable; 0·052–0·230	0·08–0·15	0·234–0·36
Diameter of sporangia	0·078–0·156	0·134–0·189	0·26–0·312
Number of sporangia per whorl	Usually 6 in all three species		
Number of sterile branches per whorl	Usually 6 in all three species		
Angle of branches to stem	90° in all three species		
Number of terminal secondary branches	Probably 4 in all three species		
Vertical distance between whorls	0·13	0·17–0·187	0·39

Cylindroporella arabica Elliott

(Pl. 6, figs. 1, 2)

1957 *Cylindroporella arabica* Elliott : 227, pl. 1, figs. 13–16.
1962 *Cylindroporella arabica* Elliott ; Powers : 131.

DESCRIPTION. This is the smallest of the Middle East species of the genus. *C. texana* Johnson, of about the same age from the U.S.A., shows smaller dimensions for internal structures but these occur in a very much longer slim segment.

HORIZON. Upper Jurassic of Arabia.

MATERIAL. *C. arabica* occurs in the upper part of the Upper Jurassic, subsurface Arab zone, in the Dukhan wells, Qatar, Persian Gulf, also at the same level in north-eastern Saudi Arabia (Powers 1962), and in Gezira no. 1 well, Murban, Abu Dhabi, Trucial Oman ; associated algae are *Clypeina jurassica* Favre and *Salpingoporella annulata* Carozzi. It occurs at the same level, also with *S. annulata*, at Al Hamiah, coastal Wahidi, Hadhramaut.

Cylindroporella sugdeni Elliott

(Pl. 6, figs. 5–7)

1957 *Cylindroporella sugdeni* Elliott : 227, pl. 1, figs. 1–6.

DESCRIPTION. This species shows large, thick segments, with greater sizes for internal structures than other species, if the Liassic *C. ellenbergeri* Lebouché & Lemoine is excepted : this last differs in various characters from the more homogeneous later species. *C. sugdeni* is proportionally shorter and much thicker than the type-species *C. barnesii*.

HORIZON. Lower Cretaceous of Middle East.

MATERIAL. Described from the subsurface Lower Cretaceous of Fahud no. 1 well, Oman, Arabia, where it was abundant. It occurs in *Orbitolina*-limestone of probable Barremian-Aptian age at Wady Hajar and Wady Ghabar, Hadhramaut : also to the north in the subsurface Lower Qamchuqa Limestone (Hauterivian level) of Kirkuk no. 116 well, Iraq.

Cylindroporella spp.

There remain various records of indeterminate *Cylindroporella*, based on random cuts in thin-section, obviously of the genus, but not diagnostic of a species : often they are small in size. These have been seen in the Lower Cretaceous Qamchuqa Formation of Chama, Mosul Liwa, northern Iraq ; subsurface in the same formation at Barremian-Aptian level in Kirkuk well no. 116, and again at this level in the Lower Cretaceous of Wady Arus, Hajar, Hadhramaut.

Genus ***CYMOPOLIA*** Lamouroux 1816

DIAGNOSIS. Thallus formed of consecutive hollow calcareous cylindrical bodies,

terminally rounded ; in each the main longitudinal canal (stem-cell cavity) extends from end to end, the wall-thickness perforated by close-set more or less horizontal whorls or verticils of branch-canals. Each verticil consisting of several branch-systems of the same pattern : an inner primary branch dividing into several (usually four) secondaries, and one sporangial cavity, usually spherical : the secondaries reach the outer surface to give a dense pore-pattern.

The dasyclad *Cymopolia* is well-known from living species in the warm waters of the East and West Indies. The plant shows a branched thallus of conventional " seaweed " pattern, in which the fronds are composed of heavily calcified serial or consecutive units, united by non-calcified tissue : each of these units corresponds in general plan to the single calcified tubes of the more normal dasyclad genera. After death the units come apart, and it is in this condition that they are met with in the fossil state, being known thus from the Upper Cretaceous onwards.

Cymopolia anadyomenea Elliott

(Pl. 7 ; Pl. 8, figs. 1, 5)

1959 *Cymopolia anadyomenea* Elliott : 218, pl. 1, figs. 1–4, 8.

Description. Elongate hollow tubular units each showing several external horizontal annular flange-like swellings or increases of diameter, more or less regularly spaced, varying in development in different individuals : external surface finely patterned with small closely-set pores. Length (incomplete), up to 6 mm. seen ; diameter varying both with absolute size and relative flange-development, 1·5–3·9 mm.(usually 2·0–2·5 mm.). Internal diameter of the main cell-cavity either constant or variable : if the latter, waxing and waning to correspond with external diameter-changes, but to a lesser extent. The d/D ratio varies correspondingly from 50–70%, being almost always 50% or more : only with extreme external flange-development can a figure of less than 50% be obtained. The wall-thickness is perforated by numerous closely-set whorls or verticils of crowded branches, 45–48 per verticil, and about 6 verticils per 1 mm. measured vertically. Each primary branch gives rise to a globular sporangium of 0·05–0·08 mm. diameter and four or more secondary branches set at an angle of 45–60° from the horizontal. The branch-systems are coarser at flange-levels, where the diameters of primary and secondary branches were 0·065 mm. and 0·039 mm. on a large specimen, and 0·039 mm. and 0·026 mm. on a small specimen.

Horizon. Maestrichtian of Northern Iraq and Afghanistan ; possibly from Maestrichtian of Tibet.

Material. Upper Aqra Formation (Maestrichtian) of Aqra and of Chalki Islam, Hadiena Formation of Chalki (top Senonian), Upper Bekhme Formation (Maestrichtian) of Chia Gara, and Aqra-Bekhme Formation of Gal-i-Mazurka, all five limestone localities in Mosul Liwa. Also in the green-rock sands (Tanjero Formation, Maestrichtian) of Diza, Erbil Liwa.

Remarks. This *Cymopolia* may be distinguished from other species of the genus by the peculiar annular flanging of the calcareous units. This " waxing-and

waning" growth suggested a half-way stage between the ordinary single tubular dasyclad and the living segmented *Cymopolia*, but it seems much more likely that the units are in fact segments themselves, as in other species, and that the frequent broken pieces found are due to ordinary post-mortem mechanical fracture. The number of sporangia per verticil (45–48) is high and gives a very crowded appearance to this fossil in section, when compared with similarly-sized *C. barbata* (L.) Lmx. (Recent) and *C. elongata* (Defr.) Mun.-Chalm. (Eocene), in both of which the count is about 30.

The flanged units give outlines of striking appearance in random thin-section. It was in this condition, recrystallized in limestones, that they attracted my attention, but no description was possible until material with the internal structures well-preserved was discovered in the green-rock sand facies of the same age. In Tibet, the *Cymopolia* sp. of Morellet (1916 : 49; Maestrichtian of Kampa Dzong) may possibly be this species, as *C. tibetica* Morellet is associated with *C. anadyomenea* in Iraq.

Although *C. anadyomenea* is thus distinctive for the Maestrichtian, an apparent homoeomorph occurs in the Lower Cretaceous of Italy (Praturlon 1964). This is not yet fully described due to scarcity of material, though it appears to differ in flange-profile. This or a similar species occurs also in the Lower Cretaceous of Borneo (Bau Formation), and in the Lower Cretaceous of Jugoslavia (Radoičić *in litt.*).

Cymopolia eochoristosporica sp. nov.

(Pl. 9, figs. 1–3)

DESCRIPTION. Tubular cylindrical thickwalled units of about 2·0–2·2 mm. external diameter (maximum seen 2·42 mm.), internal diameters 0·73–0·86 mm. (maximum seen 0·91 mm.), giving a d/D ratio of 36–40%. Estimated lengths of units up to 9 or 10 mm. Verticils of 12–14 primary branches which are probably inclined upwards at a low angle from the horizontal. Each branch communicates with the stem-cell by a very short connecting pore of 0·03–0·04 mm. diameter. These pores are set about 0·26 mm. apart measured (vertically) along the stem-cell walls. The branch then expands into the main swollen portion, seen as rounded-rectangular in near-vertical section, where it measures 0·390–0·416 mm. radially and 0·234 mm. vertically. These swollen portions occupy much of the thickness of the walls and are thus very close-set, the interstices being only 0·030 mm. thick. Finally each swollen portion divides into a small cymopoliform cluster of one spherical sporangium and four divergent secondary sterile branches. Diameter of the sporangium is 0·13 mm. ; and the diameter of the short neck or pore connecting it with the swollen primary is 0·052–0·065 mm. The secondaries have a median diameter of 0·040–0·052 mm. and expand terminally at the outer surface to shallow depressions of about 0·104 mm. diameter.

HORIZON. Maestrichtian of Trucial Oman, Arabia.

HOLOTYPE. The specimen figured in pl. 9, figs. 1, 2 from the subsurface Aruma

Formation (Maestrichtian level) of Murban No. 53 well, Abu Dhabi, Arabia. V. 52652.

SYNTYPE. The specimen figured in pl. 9, fig. 3, same locality and horizon as for holotype. V. 52653.

OTHER MATERIAL. Several incomplete random thin-sections, provenance as above.

REMARKS. This remarkable species does not at first sight appear to show the branch-structure of the genus *Cymopolia*. The large and conspicuous swollen primaries suggest a typically cladospore Mesozoic genus. However the small terminal cymopoliform branch-systems are distinctive. They are typically choristospore, and lead to the conclusion that the species shows one possible transition between cladospore and choristospore organization. Typical *C. tibetica* of the same geological age show expanded primaries, but to a very much less degree, and this feature survives not uncommonly in the Tertiary subgenus *Karreria*, and even occasionally in specimens of living *Cymopolia* (see remarks above under *C. tibetica*). In these later forms this character is best regarded as vestigial.

C. eochoristosporica appears to show the cladospore/choristospore transition by the appearance of a small choristospore development superimposed on the large cladospore branch, presumably with partial transference of sporangial contents. In this connection it is as remarkable an evolutionary record as Pia's suggested interpretation of his forms *trichophora* and *vesiculifera* of the Triassic *Diplopora annulata* as endospore and early cladospore respectively. Here the transition from endospore to cladospore is similarly considered to have taken place within the one species, but the separate characters are shown in different individuals with a possible geographical-environmental distribution of the two forms. The scarcity of my Maestrichtian *Cymopolia* spp., when compared with Pia's abundant Triassic diplopores, precludes an investigation of this possible subsidiary parallel for the present. Moreover, Herak's review of Pia's work on this subject (Pia 1920 ; Herak 1957), whilst clearing the taxonomic confusion involved, also shows the many uncertainties which attend evaluation of the Triassic species in its varied forms and occurrences, even with an abundance of material for study.

For these reasons the limited material now studied is described as a new species, the available individuals showing clearly in their morphology the characters on which the species is based.

Cymopolia tibetica Morellet

(Pl. 8, figs. 3, 4)

1916 *Cymopolia tibetica* Morellet : 47, pl. 15, fig. 10, text-figs. 14–21.
1927 *Karreria tibetica* (Morellet) Pia : 83.
1940 *Cymopolia tibetica* Morellet ; Pfender : 234.
1960 *Cymopolia tibetica* Morellet ; Elliott : 223.

DESCRIPTION (summarized from Morellet). *Cymopolia* with rather straight-sided cylindrical units of up to 2·5 mm. long and diameters from 1·1 to 1·5 mm., diameter of

central canal about 50% external diameter, external surface when unworn showing pattern of nearly uniform circular pores, but when worn showing pores of two sizes, the larger being the sporangial chambers. In the verticils, the normal branch-pattern of each primary giving rise to one spherical sporangial cavity and four secondaries is modified by the distal portion of the primary branch being greatly expanded immediately before branching into sporangium and secondaries : these additional cavities are conspicuous in vertical and transverse section.

Horizon. Maestrichtian of Tibet, northern Iraq, Turkey and Arabia.

Material. In northern Iraq, in the Aqra Formation of Aqra and of Zibar Isumeran, in the Hadiena Formation of Chalki, and in the Aqra-Hadiena development of Chalki Islam, all in Mosul Liwa, in limestone facies. The species is also known from the clastic Tanjero Formation of Diza, Erbil Liwa, and recorded by Naqib (1960 : 176), as a derived fossil, in pebbles occurring in Palaeocene conglomerates (Kolosh Formation) at Argosh, Mizuri Bala area, Mosul Liwa. Seen also in subsurface Maestrichtian at Murban, Abu Dhabi, Arabia.

Remarks. This species occurs not uncommonly in the Maestrichtian of Iraqi Kurdistan, usually in the limestone facies. Specimens are small (external diameter 0·75–0·85 mm.) and very often fragmentary, but show the distinctive characters of the species in section. The Zibar-Isumeran specimens are in the worn condition suggesting *Neomeris* or *Larvaria* as described by Morellet in some Tibetan material. The type-material was from the Maestrichtian of Kampa Dzong, Tibet : Pfender's record is from Sofular, Ankara, Turkey. She regarded both this Turkish and the type Tibetan rocks as Palaeocene. In the type area the species comes from an unequivocally Maestrichtian bed (Douvillé 1916), and it is not clear from her summary account which levels are represented at her Turkish locality. If the species was correctly determined, it seems likely that it is Maestrichtian in view of the Iraqi occurrences.

Fragmentary remains of an indeterminate *Cymopolia* sp. have also been noted in the Maestrichtian of Oman.

Pia's reference of *C. tibetica* to the Tertiary *Karreria* Munier-Chalmas was based on the former's recognition of this subgenus, not by the pyriform sporangia but by the expanded primary branches. Pfender, however, states that L. Morellet, dissecting Recent *Cymopolia*, found differences in this latter character between different segments of the same plant. In the present work *Karreria* is restricted to those Palaeocene *Cymopolia* showing pyriform sporangia.

Cymopolia kurdistanensis Elliott

(Pl. 10, figs. 2–5)

1955b *Cympolia kurdistanensis* Elliott : 127, pl. 1, figs. 13–15.
1960 *Cymopolia kurdistanensis* Elliott ; Elliott : 225.

Description. Tubular cylindrical thick-walled units with rounded ends : units variable in length and diameter relationship, length up to 4·0 mm., diameter commonly about 0·75 mm. and exceptionally up to 1·5 mm. ; internal diameter (stem-

cell) normally about 50% of external. Closely-set verticils of rather crowded branches, the internal openings of the primaries being 0·16–0·20 mm. apart measured vertically between successive whorls ; about 28 branches per verticil. Each branch shows a short primary of about 0·04 mm. diameter, directed upwards and outwards at about 60° from horizontal ; this gives rise to a single globular sporangial cavity of 0·10–0·13 mm. diameter (exceptionally larger), and to four secondary branches of 0·026 mm. diameter at their thinnest. These extend outwards and upwards at a lesser angle than the primaries, and at the outer surface they widen conspicuously to occasion the external pattern of closely-set rounded polygonal depressions of about 0·065 mm. diameter.

HORIZON. Palaeocene-Lower Eocene of Middle East.

MATERIAL. In Iraqi Kurdistan, from the Sinjar Formation of Banik and Kani Masa, Amadia (both Mosul Liwa) and Koi Sanjak (Erbil Liwa), from the Kolosh formation of Bekhme and Rowanduz (both Erbil Liwa), and from the Kolosh Formation of Surdash and Sinjar Formation of Pila Spi (both Sulemania Liwa). In southern Iraq, Basrah area, poorly preserved subsurface Palaeocene *Cymopolia* are probably of this species. *C. kurdistanensis* occurs in the Palaeocene/Lower Eocene Umm er Rhudhama Formation of the southwestern desert near Aidah, Diwaniyah Liwa. In south-east Arabia, from the Palaeocene of Jebel Abiad, and from the Batinah Coast, both Oman ; and from the Palaeocene of Jebel Faiyah, Sharjah, Trucial Oman. Very numerous fragmentary *Cymopolia* in the Palaeocene-Lower Eocene of the Middle East are probably referable to this, the commonest species.

REMARKS. *Cymopolia kurdistanensis* is a distinctive but typical species of its genus. Like the common European *C. elongata* (Defr.) Mun.-Chalm., it varies much in segment-size and proportions. It is, however, a smaller species ; L. & J. Morellet (1913 : 11) describe *C. elongata* segments as large as 12 mm. by 2·5 mm., and in this species the distance between successive whorls is larger (0·23–0·26 mm.) than found in *C. kurdistanensis*. An important difference lies in the secondary branches. The terminal widening described above for *C. kurdistanensis* does not occur in type area (Paris Basin) *C. elongata*. Hence the Middle East species shows an external pattern of shallow rounded-polygonal depressions (Pl. 10, fig. 2) whereas the European species is externally set with more abruptly-opening fine pores (Pl. 10, fig. 1). This is not a difference due to wear and tear, since abrasion of *C. kurdistanensis* would give a pattern more like that of *C. elongata*, and the European species is often perfectly preserved.

The Central American Eocene species *C. mayaense* (Johnson & Kaska, 1965) is said to be similar to *C. kurdistanensis* and *C. elongata*.

C. kurdistanensis is abundant at the localities listed and will no doubt be found elsewhere in the Middle East. Earlier Middle East records of *C. elongata* (Elliott 1955b ; 1960) are now considered to be of *kurdistanensis* (see p. 44).

Cymopolia barberae sp. nov.
(Pl. 8, fig. 2)

DESCRIPTION. Units of 0·9 mm. external diameter (up to 1·22 mm. seen) internal

diameter 43% of external, whorls showing 11 or 12 large near-spherical sporangia which occupy much of the wall-thickness, each sporangium associated with one very short primary branch and four secondaries. Diameter of the primary at the opening into the stem-cell 0·052 mm., sporangial diameter 0·130 mm., diameter of the outer expanded ends of the secondaries 0·055 mm.

HORIZON. Palaeocene-Lower Eocene of the Middle East.

HOLOTYPE. The specimen figured in pl. 8, fig. 2, from the Kolosh Formation (Palaeocene-Lower Eocene) of Surdash, Sulemania Liwa, Iraq. V. 52057.

PARATYPE. From the Sinjar Formation (Palaeocene-Lower Eocene) of Koi Sanjak, Erbil Liwa, Iraq. V. 52058.

OTHER MATERIAL. Fragments in the Palaeocene Umm er Rhudhama Formation of Al Ghurra, Wagsa, Diwaniyah Liwa, S.W. Iraq.

REMARKS. This dainty little species is uncommon ; when compared with *C. kurdistanensis* the lesser number of proportionally larger sporangia gives its characteristic appearance. Although only known in thin section it is distinctive. Its relation to *C. kurdistanensis* may be compared with that of the larger *C. rarifistulosa* L. & J. Morellet to *C. elongata*. *C. rarifistulosa*, also known from fragmentary material only, from the Miocene of Saucats, France, is described as having very large subspherical sporangial cavities, apparently less than half the number seen in *C. elongata*.

I have pleasure in dedicating this species to Mrs. Irene Barber, who has typed all my algal papers and reports.

Cymopolia elongata (Defr.) Mun.-Chalm.

(Pl. 10, fig. 1)

1955b *Cymopolia* cf. *elongata* (Defr.) ; Elliott : 126.
1960 *Cymopolia elongata* (Defr.) ; Elliott : 225.

Re-examination of the numerous specimens from the Iraqi and Arabian Palaeocene/Lower Eocene, formerly referred to *C. elongata*, has shown that many may be identified as near-vertical cuts tangential to the inner surface (stem-cell surface) of *C. kurdistanensis*, or as fragments of examples showing the terminally-widening secondaries of *C. kurdistanensis*. The remainder comprises random cuts of *Cymopolia* sp. which are more likely to be *C. kurdistanensis* from their associations.

It is therefore concluded that the true *C. elongata* has not been met with in the Middle East collections studied, and that *kurdistanensis* is the typical and common Palaeocene and Eocene species of *Cymopolia* there, as *elongata* is in Europe.

Cymopolia (Karreria) sp.

(Pl. 10, fig. 6)

1955b *Cymopolia* (*Karreria*) sp. ; Elliott : 126.

DESCRIPTION. Units of about 0·73 mm. external diameter and 0·39 mm. internal

diameter, with whorls showing about 20 radially elongate, subpyriform sporangia of 0·156 mm. by 0·090 mm. each communicating with the interior by a very short primary branch, which also divides into four secondaries.

HORIZON. Palaeocene-Lower Eocene of Iraqi Kurdistan.

MATERIAL. Fragmentary thin-section material from the Kolosh Formation (Lower Eocene) of Surdash, and from the Sinjar Formation (Palaeocene-Lower Eocene) of Pila Spi, both Sulemania Liwa ; from probable Sinjar Formation, Sedelan, near Sulemania ; all localities in Iraqi Kurdistan.

REMARKS. This species is smaller than *Cymopolia* (*Karreria*) *zitteli* L. & J. Morellet from the Paris Basin Middle Eocene, shows fewer sporangia (20 against 24), and is proportionally thicker walled. By reason of the fragmentary nature of the material, the innermost layer of the wall, dividing the central stemcell from the cavities of the expanded primary branches, is usually missing. Although from the available evidence this is very probably a new species, it cannot be described as such from this material.

Genus ***DACTYLOPORA*** Lamarck 1816

1940 *Dactylopora anatolica* Pfender : 237.
1966b *Dactylopora anatolica* Pfender ; Massieux : 118, pl. 3, figs. 1–3.

This large and handsome dasyclad, well-known from the Paris Basin Eocene, has not been met with in the collections studied by me, and the only Middle East record appears to be that of Pfender, quoted above, for the top Cretaceous (or possibly Palaeocene) of Turkey (Lutetian according to Massieux, but see p. 42 above).

Genus ***DIPLOPORA*** Schafhäutl 1863

1960 *Diplopora* spp. Elliott : 219, 221.

The rich Triassic diplopore-limestones of central Europe and the Balkans are largely missing from the Middle East, at any rate from the areas studied by me. Although a thick development of marine Trias occurs in both Iraqi Kurdistan and Oman, original facies and subsequent dolomitization have combined to make these rocks almost completely barren of dasyclads.

The Upper Triassic Elphinstone group in Peninsular Oman yielded two alleged dasyclads during thin-section studies by M. Chatton, one of which was recorded (Elliott 1960) as *Diplopora* cf. *phanerospora* Pia. A re-examination of these specimens shows that they may not be dasyclads, and appear indeterminable. The evidence for R. G. S. Hudson's records of *Diplopora* as " not uncommon " and " occurs throughout " in different beds of the Asfal Formation of the Elphinstone Group (Hudson 1960 : 304) is not known to me, as Hudson did not make these extensive collections available for the study of the algae.

Diplopora sp. was also recorded (Elliott 1960) from the north Iraqi Permian. Although species of the genus have been described from the Permian of Japan, Turkey (Güvenç 1965) and elsewhere, the Iraqi specimens appear on re-examination not to be diplopores.

Genus *DISSOCLADELLA* Pia 1936

DIAGNOSIS. Small tubular dasyclads, usually thin-walled with wide stem-cell cavity and often annular, each verticil showing horizontal branches with a short distally-swollen primary dividing into a bunch of short secondaries, usually four in number and terminally widening.

Dissocladella deserta sp. nov.

(Pl. 10, figs. 7, 8)

1960 *Dissocladella* sp. Elliott : 225.

DESCRIPTION. Small hollow calcareous cylinder, straight-sided with rounded ends, length about 0·75 mm., external diameter 0·39–0·47 mm., internal diameter 0·23–0·29 mm., verticils of about twelve branches each set 0·13 mm. apart vertically; branches showing a short primary, swollen to varying degree, and then dividing into four straight divergent secondaries which widen terminally to external pores.

HORIZON. Palaeocene and Eocene of the Middle East.

SYNTYPES. The specimens figured in pl. 10, figs. 7, 8, from the Umm er Radhuma (Palaeocene-Lower Eocene) Formation of Wagsa and Aidah, Diwaniyah Liwa, S.W. Iraq. V. 52066, 67.

OTHER MATERIAL. Very numerous random thin-sections from the same horizon and general area, and subsurface in the Basra oilfields, S. Iraq. Also from the Palaeocene Seiyan limestone of Wady Ghabar, Hadhramaut, S. Arabia. It may occur in the Lower Eocene of Egypt (see below).

REMARKS. This little *Dissocladella*, although very common, occurs in a porous microcrystalline dolomitic limestone and is always very poorly preserved, the structures showing as cavity-patterns amongst the pores and crystals. Although recognized some years ago, better material has not been found, and it is now described. It may well be the same as the " *Dactylopora* " sp. of Schwager (1883) from the Lower Eocene " Libyschen-Stufe " of Egypt, as remarked by Pia (1936b); the latter's comment on the relative sizes is an error.

Dissocladella undulata (Raineri) Pia

(Pl. 11, figs. 4–6)

1936a *Dissocladella undulata* (Raineri) var. ; Pia : 4, pl. 1.
1960 *Dissocladella undulata* (Raineri) ; Elliott : 224.
1966b *Dissocladella undulata* Raineri ; Massieux : 115, pl. 2, figs. 2, 3.

DESCRIPTION (detail after Pia). Small hollow calcareous cylinder, length about 1·4 mm., external diameter 0·24–0·32 mm., internal diameter 0·08–0·10 mm., with close-set verticils showing about 8 primary branches. These are narrow at the junction with the stem-cell and widen outwards, finally dividing into about six secondaries of similar shape which widen to the outer surface.

HORIZON. Upper Cretaceous, North Africa, Western Mediterranean and Middle East.

MATERIAL. From the subsurface Turonian of Musaiyib well, Hilla Liwa, Iraq ; also from the subsurface Turonian of Ras Sadr Well, Trucial Oman, Arabia.

REMARKS. This little alga was described by Pia from the Cenomanian-Turonian of Libya. In the Middle East, at the two localities given above, it is fragmentary and very poorly-preserved, but in both cases is associated with *Trinocladus tripolitanus* Raineri and the codiacid *Boueina pygmaea* Pia as at the type-locality ; the range of this little algal microflorule is therefore Upper Cretaceous.

Dissocladella sp.

Fragments of a small dasyclad showing branching of *Dissocladella* pattern have been noted in the north Iraq Maestrichtian, but are insufficient for description as a species. The occurrences are in the Tanjero Clastic Formation at Balambo (Sulemania Liwa), in the Aqra/Hadiena Limestone of Chalki Islam (Mosul Liwa), and in the subsurface Formation of Makhul no. 1 well (Mosul Liwa).

Dissocladella savitriae Pia

(Pl. 11, figs. 1–3)

1936b *Dissocladella savitriae* Pia : 15, pl. 1, figs. 1–4, pl. 2, fig. 4, text-figs. 1–9.
1955b *Dissocladella savitriae* Pia ; Elliott : 126, 128, pl. 1, fig. 2.

DESCRIPTION. Thin-walled hollow calcareous cylinder, length of maximum fragment observed, 3·5 mm. ; (estimated length in life, up to 17 mm.), external diameter up to 1·7 mm., internal diameter from 69–78% of external in specimens measured, frequently about 71%. Successive verticils are represented by thin superimposed consecutive rings, of thickness up to 0·21 mm., feebly cemented together, which readily come apart and are themselves intrinsically fragile from their proportions. Rings are straight-sided within, convex without, giving the thallus an annular appearance externally. Each ring contains up to 44 globular or bluntly ovoid sporangial swellings of up to 0·13 mm. diameter : these are connected to the interior by a short primary canal of 0·026 mm. diameter and to the exterior by several bunched secondaries (4–6 from the type-description ; Middle East material does not conflict with this). The secondaries are from the sporangial swelling itself, not from the primary ; they are about 0·013 mm. in diameter and they widen to emerge on the external surface as pores.

HORIZON. Palaeocene of Middle East ; " Danian " of India.

MATERIAL. Solid specimens (broken tubes) and random thin-sections from numerous localities. In Iraqi Kurdistan, from the Sinjar Formation (Palaeocene-Lower Eocene) of Banik (Mosul Liwa), Kolosh Formation (Palaeocene-Lower Eocene) of Bekhme and of Rowanduz (Erbil Liwa), and of Surdash (Sulemania Liwa). Probably present (very poor preservation) in the Palaeocene limestones of the south-western desert, Iraq. In Arabia, from the subsurface Lower Eocene, Dukhan no. 3

well, Qatar Peninsula ; from the Palaeocene of Jebel Faiyah, Trucial Oman ; and from the Palaeocene of the Batinah Coast, Oman.

REMARKS. This species was first described in great detail by Pia (1936b), his material coming from the Trichinopoly Danian, India (now regarded as Palaeocene). The Middle East material confirms his description, and also his reconstruction of the exterior, as all his material was in thin-section. His delightful reconstruction of the living algae in association with others (*op. cit.*, fig. 43) appears reasonable from the extensive Middle East material studied. It should be noted that for algae at any rate, the Tethyan Palaeocene appears to commence immediately after the Maestrichtian, the flora (including *D. savitriae*) extending up into the Lower Eocene ; this point is discussed in more detail later in this work.

Genus ***EOGONIOLINA*** Endo

1953a *Eogoniolina johnsoni* Endo : 97–104, pl. 9, figs. 5–10.
1960 *Engoniolina johnsoni* Endo (*lapsus calami*) ; Elliott : 219.

REMARKS. As described by Endo, the Permian *Eogoniolina* was a club-shaped dasyclad with a lower, long cylindrical stem-like portion which extended up to a terminal expanded globular portion : this is well-shown in his reconstruction (*op. cit.*, text-fig. p. 102). His microphotographs, however, in this and later papers, usually show the pear-shaped or pyriform terminal portion only, and it was by comparison with this that the species was recognized in the Iraqi Permian by me. Subsequent re-study of this material shows that these specimens are in fact pyriform segments of *Mizzia velebitana*. At both the Iraqi and Japanese localities normal spherical examples of this common species are abundant. Without prejudice to Endo's interpretation of his original Japanese material, the Iraqi record is therefore withdrawn. *Eogoniolina pamiri* has been described from the Turkish Permian (Güvenç 1966b).

Genus ***EPIMASTOPORA*** Pia 1923

DIAGNOSIS (emend. after Endo). Similar to *Pseudoepimastopora*, but with relatively long pores having the same width throughout their length.

" ***Epimastopora minima*** Elliott " (= ***Tauridium*** sp.)

1956 *Epimastopora minima* Elliott : 327, pl. 1, figs. 1, 3.

This species was founded on fragmentary remains which occur abundantly in samples from at or near the base of the Satina Formation, or the middle evaporitic unit of the Chia Zairi or Iraqi Permian. The original remains are almost comminuted, and a re-examination in the light of subsequent studies on *Epimastopora* and *Pseudoepimastopora* suggested that the original generic allocation is doubtful. The description of the codiacid genus *Tauridium* (Güvenç 1966a) shows clearly that the Iraqi fossils are debris of a species of this genus, and not remains of a dasyclad.

Epimastopora sp.

Fragmentary remains referred to the genus are said by Rezak (1959) to be abundant in the upper part of the Permian Khuff Formation (probably Upper Permian) of Dammam no. 43 well, Saudi Arabia.

Genus *FURCOPORELLA* Pia 1918

DIAGNOSIS. Cylindrical dasyclad tube with successive verticils of horizontal paired straight radially divergent branches ; each pair of branches commences at a single opening on the interior : bifurcation occurs almost at once and the two divergent secondaries extend to the exterior.

Furcoporella diplopora Pia

(Pl. 11, figs. 7–9)

1918 *Furcoporella diplopora* Pia : 209, pl. 1, figs. 1, 2 ; text-fig. 46.
1940 *Furcoporella diplopora* Pia ; Pfender : 242.
1956 *Furcoporella diplopora* Pia ; Elliott : 332, pl. 2, figs. 5, 6.
1960 *Furcoporella diplopora* Pia ; Elliott : 225.
1966 *Furcoporella diplopora* Pia ; Massieux : 121, fig. 4, pl. 4, figs. 8, 9.

DESCRIPTION. Hollow cylindrical calcareous tube, long and straight-sided ; length (incomplete) up to 5·0 mm. seen, with external diameter of up to 0·6 mm., and corresponding internal diameter of 0·325 mm. ; d/D ratio on smaller specimens from 48–55%. Numerous regular horizontally-set verticils of paired branches ; about 11 per mm. of tube-length. Each verticil shows about 8 pairs, each commencing on the inside of the tube as a single large pore : in transverse section the very short primary canal is seen to divide at once into two secondaries, which diverge at an obtuse angle varying from 45–70° and proceed, widening slightly, in a straight course to the periphery where they widen sharply to emerge as external pores. In vertical section only a succession of straight, coarse, waisted pores is seen ; in an oblique vertical cut the plane of section, traversing successive near-identical pore-pairs outwards, shows that the canals widen transversely but not vertically before splitting into two.

HORIZON. Middle Eocene of Central and Southern Europe : Palaeocene and Eocene of Middle East.

MATERIAL. In Iraqi Kurdistan, from the Sinjar Formation (Palaeocene-Lower Eocene) of Banik and (subsurface) Gullar no. 1 well (both Mosul Liwa) and Kashti (Sulemania Liwa) ; from the Kolosh Formation (Palaeocene-Lower Eocene) of Rowanduz and Koi Sanjak (both Erbil Liwa), and of Sedelan (Sulemania Liwa). In southern Iraq, fragmentary and ill-preserved remains from the Palaeocene Ghurra Beds of the Umm er Rhudhama Formation, Wagsa (Diwaniyeh Liwa) and elsewhere in the southwestern Iraqi desert. In Arabia, from the Palaeocene-Lower Eocene of the Batinah Coast, Oman ; from the Palaeocene of Jol Ba Hawar, and the Palaeocene-Lower Eocene of Aqabar Khemer, Hajar, both Hadhramaut. See also Hadhramaut record of Beydoun (1960 : 146).

REMARKS. Pia's type-material was from the Austrian Middle Eocene ; the species also occurs in the Middle Eocene of Egypt and Syria (Pfender 1940), Iraq (Sulemania district), and South Oman (Jebel Tanamir). The Middle Eastern Palaeocene-Lower Eocene examples listed above correspond in structure to the type material, but reach a larger size in many if not all examples. External diameters quoted by Pia and Pfender, for example, are 0·26–0·34 mm. and 0·35–0·45 mm respectively, whilst the older Iraqi material described above may attain a corresponding dimension of 0·6 mm.

Although *F. diplopora* is represented fossil by stout calcareous tubes, the structures preserved afford but an imperfect record of those of the living plant. The larger examples are no better than the smaller in this respect. All indicate a very short primary branch and two secondaries : presumably these latter, which are seen to expand as they reach the outer edge of the zone of calcification, branched further into a spray of uncalcified tertiary branchlets : there is no evidence at all of the sporangia. The relationships of the genus remain doubtful.

Genus ***GRIPHOPORELLA*** Pia 1915

DIAGNOSIS. Very thin-walled cylindrical, club or ovoid shaped dasyclad calcifications, with numerous simple perforations ; so thin-walled that the perforation-structures are insufficient for elucidation of the branch-structure.

REMARKS. *Griphoporella* is an inclusive name for those dasyclads whose calcification was confined to a thin hood-like sheet which affords no clue to the detailed branch-structure, size of stem-cell, etc. of the original plant. The species referred to it range from Triassic to Palaeocene and may be quite unrelated phylogenetically; see especially under *G. arabica* below.

Griphoporella cf. ***perforatissima*** Carozzi

(Pl. 12, fig. 4)

1955b *Griphoporella perforatissima* Carozzi : 203, text-fig. 1a–d.
1960 *Griphoporella perforatissima* Carozzi ; Elliott : 223.

DESCRIPTION. See under remarks.

HORIZON. Top Jurassic and bottom Cretaceous of Europe and Middle East.

MATERIAL. Fragments from the subsurface Upper Jurassic Najmah Formation of Kirkuk Well no. 117, Iraq ; in Arabia, from top Jurassic and bottom Cretaceous levels at Haushi, Southern Oman, and from the Lower Cretaceous of Burun, Wady Hiru Basin, Hadhramaut.

REMARKS. The material listed above is extremely fragmentary, but is of a thin-walled dasyclad, circular in cross-section, and showing very many simple pores. It is similar in age-occurrence to Carozzi's *G. perforatissima* (Portlandian-Berriasian), and has a similar appearance in random cut to the type-figures (Carozzi 1955b, fig. 1a). The pores are 0·030–0·040 mm. in diameter, and about 0·020 mm. apart. This is larger than in *G. perforatissima* (0·015–0·019 mm. diameter set 0·009–0·012 apart),

and would give a pore-count per square millimetre of about one third that quoted for the type. It is however closest to this rather than to the other Upper Jurassic species *G. undulata* Pia, *G. irregularis* Pia and *G. ehrenbergi* Bachmeyer (comparison-table of Carozzi, *op. cit.*, : 206). In view of this correspondence, and of the inadequacy of the Middle East material for full description, it is given the qualified determination above.

" *Griphoporella arabica* Pfender 1938 "
(*Ovulites maillolensis* Massieux)

(Pl. 12, figs. 1, 3)

1938 *Griphoporella arabica* Pfender : 69, pl. 9, figs. 5–8.
1940 *Griphoporella arabica* Pfender ; Pfender : 241.
1955b *Griphoporella arabica* Pfender ; Elliott : 126.
1966a *Ovulites maillolensis* Massieux ; Massieux : 241, pls. 1, 2.

DESCRIPTION. Broadly club-shaped or elongate-ovoid, thin-walled, hollow calcification, external diameter up to 0·9 mm., length not known but at least three times diameter from oblique-longitudinal sections. Wall thickness up to 0·078 mm., perforated by close-set straight-sided pores of about 0·013 mm. diameter, widening very slightly at the external surface, and set 0·006–0·013 mm. apart as seen in section.

HORIZON. Paleocene and Eocene of France, North Africa and Middle East.

MATERIAL. In Iraqi Kurdistan, from the Kolosh Formation of Koi Sanjak (Erbil Liwa) and from the Sinjar Formation of Sirwan (Sulemania Liwa), both Palaeocene-Lower Eocene. In Arabia, from the Palaeocene-Lower Eocene of Sahil Maleh, Batinah Coast, Oman, and from the Seyun Limestone development of the Umm er Rhudhama Formation (Palaeocene) of Ma'adi Pass, east of the Mukulla-Shihr road, Hadhramaut.

REMARKS. The species was described by Pfender from the Lower Eocene of Morocco, and recorded by her from the Middle Eocene of Egypt and Syria ; a related species was mentioned from Madagascar. Pfender's specimens were smaller, with external diameters of up to 0·4–0·58 mm., and thinner-walled (0·040–0·050 mm. wall-thickness), but the pores and pore-spacing were similar, and it seems unnecessary to refer the Middle East specimens to a new species because some individuals attain a larger size.

In her type-description of the French Lower Eocene codiacean *Ovulites maillolensis* Massieux (1966a) records that from preliminary studies on thin-sections she determined this species as *Griphoporella arabica* Pfender. Further studies on whole (isolated) segments or articles, and comparison with the classic and beautifully-preserved Paris Basin species (Munier-Chalmas 1881) convinced her that these fossils were remains of *Ovulites*, as was also Pfender's North African material. The new species was created as Pfender's type-material could not be traced and the original description was inadequate in view of the new evidence available.

I agree with Mlle. Massieux's conclusions. The Middle Eastern material described above was identified by comparison with Pfender's accounts (1938 : 1940), and is

well-known in the literature as *G. arabica*. It shows no diagnostic dasyclad characters to refute the new allocation (and indeed the genus *Griphoporella* itself is a receptacle for various inconclusive dasyclads, probably not closely related). The description of this codiacean is retained here for comparison with dasyclads as, unlike the problematic *Thaumatoporella*, it is well-known in dasyclad literature.

Genus *GYROPORELLA* Gümbel 1872

1960 *Gyroporella* cf. *maxima* Pia ; Elliott : 219.

Many Permian species of *Gyroporella* have been described from Japan, also one from the U.S.A. (Johnson 1963), and one from Turkey (*Gyroporella* sp., Bilgütay 1959). My record of *G.* cf. *maxima* from Iraqi Kurdistan was based on a single random section : no further material has been found to substantiate this, and the determination is therefore abandoned.

Genus *INDOPOLIA* Pia 1936

DIAGNOSIS. Calcareous tubular dasycladacean showing verticils of branches each of which consists of one primary dividing into two secondaries set one above the other (vertically) : in fertile whorls each branch gives rise to two sporangia.

Indopolia satyavanti Pia

(Pl. 12, fig. 2)

1936 *Indopolia satyavanti* Pia : 20, pl. 1, figs. 1, 5–13, text-figs. 17–19.

DESCRIPTION (details after Pia). Hollow calcareous elongate tubes, length unknown but perhaps 5·0 mm. or more ; external diameter (fertile part) 0·86–1·16 mm., with internal diameter of 44–49% external ; (sterile part) 0·55–0·98 mm. external, internal 47–55%. Fertile whorls of perhaps 28 branches ; each branch consists of one primary, which is set obliquely at 60–70° from the horizontal : this divides into two secondaries set nearly horizontally one above the other and reaching the outer surface almost horizontally i.e. nearly at right angles to it. The secondaries increase in diameter to become funnel-shaped and almost in contact at the external surface, and occasion a polygonal pattern there. Two small pyriform sporangia (diameter 0·09–0·12 mm.) are attached at or near the branch-junctions. The sterile whorls do not of course show sporangia, but the branches are similar.

HORIZON. " Danian " of India ; Palaeocene of Middle East.

MATERIAL. In Iraqi Kurdistan, from the Sinjar Formation (Palaeocene-Lower Eocene) of Banik, Mosul Liwa, where it is uncommon. Possibly also in Arabia, from the Upper Palaeocene of the Batinah Coast, Oman (poorly preserved).

REMARKS. Pia's material was from the Trichinopoly Danian of India, where the species was abundant and described as the " almost constant companion of *Dissocladella savitriae* ". In the Middle East, although *D. savitriae* is widespread, and

with it the non-dasyclad alga *Parachaetetes asvapatii* Pia, also described from the same Indian locality, *Indopolia* is very rare. In Kurdistan it was found in the present investigation only at Banik, and there is possibly one other record from Oman (see above).

The Banik material shows sterile whorls only. A measured example has an external diameter of 0·455 mm., and internal diameter of 0·221 mm., or 49% ; although a little smaller, the section is closely similar to that of a sterile specimen figured from the type-material (Pia 1936b, pl. 1, fig. 11).

Although the algal sampling for the present study was far from exhaustive, the poor showing of *Indopolia* in the Middle East, when compared with its Indian associates *Dissocladella* and *Parachaetetes* is probably significant. The rare occurrence, of sterile remains only so far, suggests that it did not manage to spread westwards along Tethyan coasts. *Indopolia feddeni* Rao & Vimal (1955) is uncommon in the Palaeocene of Pakistan. Perhaps *I. satyavanti* is replaced in the algal economy by the prolific *Cymopolia kurdistanensis*, not known from the Trichinopoly beds.

Genus *LARVARIA* Defrance 1822

1960 *Larvaria* sp. Elliott : 223.

The writer's 1960 record of *Larvaria* sp. from the Kurdistan Maestrichtian, is based on a worn example of *Cymopolia tibetica* Morellet (see above, under *C. tibetica*). *Larvaria* sp. was recorded by Barthoux (1920) from the Lower Eocene of Suez, Egypt.

Genus *MACROPORELLA* Pia 1912

1960 *Macroporella* sp. Elliott : 219, 221.

My 1960 records of this genus, from the Permian of Iraqi Kurdistan and from the subsurface Upper Triassic of Qalian no. 1 well, Mosul Liwa, Iraq, were made on scarce and poorly-preserved material. No further specimens of either have been found. The Permian record is now discounted, and the Triassic one remains very doubtful.

Jurassic and Cretaceous species formerly referred to this genus are now described under *Pianella* and *Acroporella*.

Genus *MORELLETPORA* Varma 1950

1950 *Morelletpora nammalensis* Varma : 207, figs. 1, 2.
1955 *Morelletpora nammelensis* Varma ; Varma : 101–111, 2 pls.
1960 ?*Morelletpora nammelensis* Varma ; Elliott : 225.

My 1960 record of this species (a queried determination) from the Palaeocene-Lower Eocene of Iraq, based on a random section, proves to be from material of Middle Eocene age and is not further dealt with here.

Genus ***MIZZIA*** Schubert 1907

1907 *Mizzia* Schubert : 212.
1908 *Mizzia velebitana* Schubert : 382, pl. 16, figs. 8–12.
1920 *Mizzia* Schubert ; Pia : 18.
1942 *Mizzia* Schubert ; Johnson and Dorr : 63.
1959b *Mizzia* Schubert (emend) ; Rezak : 534.

Diagnosis (after Rezak). " The thallus is composed of segments joined end to end in a loosely articulated fashion. The segments are generally disaggregated and are rarely found joined together like a string of beads. Individual segments are spheroidal to cylindroidal or pyriform and are composed of a central cavity (generally barrel-shaped) through which the stipe extended. Radiating from the central cavity are simple expanding, unbranched rays arranged in regular, alternating horizontal rows. At the periphery of the segment the expanded rays are in mutual contact. The alternating nature of the rays and their crowding at the periphery gives rise to a hexagonal (honeycomb) pattern on the surface of each segment. Species are based on shapes and dimensions of the segments and their internal structures ".

Mizzia velebitana Schubert 1908

(Pls. 13, 14)

1908 *Mizzia velebitana* Schubert : 382, pl. 16, figs. 8–12, text-fig. 5.
1933 *Mizzia velebitana* Schubert ; Kühn : 155.
1955a *Mizzia velebitana* Schubert ; Elliott : 83.
1959b *Mizzia velebitana* (Schubert) emend. Rezak ; Rezak : 536, pl. 72, figs. 1–3, 5, 6, 8–10, 12, 13, 15–19.
1959 *Mizzia velebitana* Schubert ; Bilgütay : 49, pl. 1, figs. 2–3, pl. 2, fig. 1.
1960 *Mizzia velebitana* Schubert ; Elliott : 219.

Description (from Iraqi material). Hollow, calcareous, bead-like segments, spheroidal, ovoid or elongate-ovoid, pear-shaped or pyriform ; length up to 2·0 mm., external diameter (maximum) up to 2·25 mm., internal diameter measured in the same transverse plane, 60–70% of external ; polar (proximal and distal) openings or gaps in the segment, from 0·18–0·36 mm. diameter in a large segment. Wall perforated by about 12 successive horizontal verticils of coarse pores (short branches), usually 20–25 per verticil over all but the polar ends of the segment. The pores of each verticil are set alternately to those of adjacent verticils, to give the external and surface-tangential section appearance of a large closely-set hexagonal mesh. In vertical section the branches are seen to be wedge-shaped, widening slowly from interior to exterior, and usually of about 0·18 mm. diameter in large examples. Externally the pores may be open or closed : in the latter case they are roofed by a thin externally-convex projecting calcareous covering.

Horizon. Permian ; North America, North Africa, Europe, Asia.

Material. In Iraq, common throughout most of the thickness of the Zinnar Formation and the Darari Formation, and occurring rarely in the intermediate Satina Evaporite Formation ; that is, probably from within the upper part of the Lower Permian to near the top of the Upper Permian (but see under Stratigraphic

Ranges) : abundant over this range in much of the material from the sampled surface sections of Ora and Harur, Mosul Liwa, and also from subsurface Upper Permian in Atshan no. 1 well, in the south of Mosul Liwa (see Hudson 1958 ; Dunnington, Wetzel & Morton 1959). Elsewhere in the Middle East Permian recorded by Kühn (1933) from Iran, by Bilgütay (1959) and Güvenç (1965) from Turkey and by Rezak (1959b) from Saudi Arabia.

REMARKS. *Mizzia velebitana* is a characteristic Permian microfossil of circum-global distribution : central and southeastern Europe and north Africa, the Middle East, Sumatra and Japan, and the southwestern United States. Its distribution was plotted and compared by Pia (1937) with that of the living warm-water codiacid alga *Halimeda tuna* Lmx. Extensive bibliographies of these occurrences have been given by Pia (1937), Johnson & Dorr (1942) and Rezak (1959b) : that given above refers mostly to the Middle East occurrencies.

Rezak (*op. cit.*) has discussed the genus and type-species in detail, and given revised diagnoses for them. That for the genus is quoted above in full : the description given here is based on the material from Iraqi Kurdistan studied by me. When compared with the equivalent species-diagnosis of Rezak, which was a synthesis of previous records and his own study of Saudi Arabian material, it is seen that the Iraqi specimens do not attain the maximum size (length breadth and pore-diameter) quoted for the species elsewhere, but are larger in size and equal in pore-diameter to the Saudi Arabian specimens.

Rezak transferred *Mizzia* to the dasyclad tribe Diploporeae, after clear demonstration of the regular arrangement of the side-branches : I agree with this. All previous workers have followed Schubert (1908 : 383) in supposing the stem-cell in each globular *Mizzia*-segment to have filled the central cavity, so that the primitive unbranched side-branches commenced approximately where the inner calcareous wall is seen in the fossil (e.g. Pia 1920 : 21 ; Rezak 1959 : 534). Theoretically it is possible that a thinner central stem-cell gave rise to thin radiating branches which thickened terminally and were calcified only around the thicker peripheral portions: a comparable arrangement exists in the Recent *Bornetella*. Although this is a much more complex dasyclad than the Permian *Mizzia* is believed to have been, it was the comparison-genus used by Wood (1943) in reconstructing the non-calcified parts of the still older dasyclad *Koninckopora* from the Carboniferous. However, the serial arrangement of connected *Mizzia*-segments (a phenomenon known from occasional short strings of consecutive fossil segments from various localities, though not yet from Iraq) is believed to indicate a jointed plant somewhat like the living *Cymopolia* (Pia 1920 ; Rezak 1959b). Mechanically, the *Bornetella*-interpretation would result in segments which would probably be extremely fragile for the assumed mode of life of *Mizzia*, even in quiet waters : *Bornetella* itself is a single non-segmented dasyclad, attached by a short holdfast. It therefore seems more likely, though not definitely known, that the older interpretation is correct. Taken in conjunction with the abundance of the fossil segments and their wide distribution, this would make *Mizzia* a common dasyclad of primitive structure, vigorous growth, and thick juicy stem-cell. This is consistent with the picture set out in the section on ecology.

Several species, other than the type-species, have been described for *Mizzia* : e.g. *M. yabei* Karpinsky, *M. japonica* Karpinsky, *M. minuta* Johnson and Dorr, *M. bramkampi* Rezak, *M. cornuta* Kochansky and Herak. These are based primarily on differences in segment shape and size, and sometimes on branch-structure. Morphologically such species are recognizable taxonomic entities. However, usually they seem to be associated with *M. velebitana*, and, so far as one can tell from the literature, to be also a minority of the local *Mizzia*-populations. Bearing in mind the variation of segments within a plant, and the environmental local variations in plant-populations, as evidenced by the study of Hillis (1959) on Recent *Halimeda*, the genus with which Pia compared *Mizzia* for distribution, it is felt that mostly they may well be, in the botanical sense, of varietal status at best. *M. bramkampi* Rezak, with its distinctive funnel-shaped branch-structure, appears the one most likely to be a distinct local species. This was described from Saudi Arabia (Khuff formation ; probably Upper Permian) : other species recorded from the Middle East are *Mizzia yabei* and *M. minuta* from Turkey (Bilgütay 1959) ; also *M. tauridiana* (Güvenç 1965).

All the Iraqi Kurdistan specimens seen are referred here to *M. velebitana.* Occasional specimens resembling *M. yabei* are considered atypical segments of the type-species. One or two specimens resemble some of Endo's figured *Eogoniolina*, but not his reconstruction, and there is no associated evidence to show that these are other than *M. velebitana.* Also in the Iraqi material are various specimens corresponding to *M. cornuta* Kochansky & Herak (1960), a species in which the external bulging terminations of the branches (or pores) are roofed over by a thin projecting convex calcareous covering. Setting aside worn material, and many fossil *Mizzia* segments are recognizably abraded, it would seem that in apparently well-preserved material the pores can be open or closed. This point was discussed in some detail by Pia (1920), who suggested that this difference in the otherwise homogeneous assemblage of segments might possibly be due to the covered pores having contained sporangia. He also drew attention to the effect of light-intensity, varied by shading due to stones, etc. on the calcification of living algae, and to the differences in the calcification of the older and younger segments of the same plant. I believe that in the case of *Mizzia* light intensity may have influenced this calcification ; in view of what is known of this phenomenon in modern algae, and the random distribution of specimens with roofed pores in *Mizzia*, the character does not seem worthy of occasioning a distinct specific name. It is true that Kochansky & Herak (*op. cit.*, text-fig. 7) give a longer range for *M. cornuta* than for *M. velebitana* in the Jugoslav Permian, but in Iraq at any rate *M. cornuta* is represented by a small minority of specimens within the main range of *M. velebitana.*

Genus ***MUNIERIA*** Deecke 1883

DIAGNOSIS. Dasyclad with thin central stem-cell giving rise to regularly and widely spaced verticils of thin straight horizontal radial side-branches, the whole thickly calcified to give a rigid structure of centrally fused calcified successive whorls.

Munieria baconica Deecke

(Pl. 15, figs. 3–8)

1883 *Munieria baconica* Deecke : 9, pl. 1, figs. 4–8.
1920 *Munieria baconica* Hantk. ; Pia : 144, pl. 7, figs. 16–26, text-fig. 25.
1948 *Munieria baconica* Hantk. ; Carozzi : 351, pl. 6, fig. 3, text-fig. 48.
1955b *Munieria baconica* Deecke ; Elliott : 126.
1955a *Munieria baconica* Deecke ; Carozzi : 47, text-figs. 10–12.
1958a *Munieria baconica* Deecke ; Elliott : 255, pl. 45, fig. 4.
1958 *Munieria baconica* Deecke ; Radoičić : 79, pl. 1, text-figs. 2, 3.
1960 *Munieria baconica* Deecke ; Elliott : 223, 224.
1962 *Munieria baconica* Hantken ; Delmas & Deloffre : 216, pl. 3.

Description (based on Pia and Carozzi). Dasyclad with external diameter (at verticil-level) of 0·6–1·6 mm., internal diameter (stem-cell) of 0·05–0·26 mm. ; verticils set apart at distances of about 66% of their diameter. Each verticil horizontal, consisting of about 16 straight radial simple branches of about 0·08–0·09 mm. median diameter. Verticils and stem-cell thickly calcified, to give successive thick horizontal discs at verticil level, joined to the thick stem-cell calcification. Occasionally calcification unites the discs peripherally.

Horizon. Upper Jurassic–bottom Cretaceous of Switzerland and Jura ; top Albian of France (Delmas & Deloffre 1962) ; Upper Jurassic–Lower Cretaceous of Italy (Sartoni and Crescenti 1962). Lower Cretaceous of Spain, central and south-eastern Europe and Middle East.

Material. In the Middle East, probably common but always fragmentary. Seen in the Lower Cretaceous of Iraqi Kurdistan, Barremian to Aptian : Sarmord Formation, Barremian level, and Qamchuqa Formation, Albian level of Surdash (Sulemania Liwa) ; Qamchuqa Formation of Ru Kuchuk and Rowanduz, Mosul and Erbil Liwas and Zibar-Isumeran, Mosul Liwa ; Aptian, Albian and Barremian–Aptian levels respectively. In southern Arabia, Lower Cretaceous of Hadhramaut (e.g. Mintaq, Wady Hajar ; Barremian–Aptian), and Lower Cretaceous of Oman (e.g. Haushi, South Oman).

Remarks. Originally described by Deecke (1883) from the Aptian of Hungary. Later Pia (1920) attempted a reconstruction of this alga from thin-section material. Carozzi (1948 ; 1955a), gave line drawings of random sections of Swiss material : he recorded it from Upper Kimmeridgian to Valanginian. Radoičić (1958) gave excellent photographs of random sections of Jugoslav material from the Valanginian-Hauterivian.

My Middle East records (Elliott 1955b ; 1958a ; 1960) record the species from Barremian to Albian.

This Middle East material is extremely fragmentary. It occurs in the Lower Cretaceous " debris-facies " (Elliott 1958a), an off-shore deposit in which small calcareous scraps, largely algal, form an appreciable part of the sediment. Much of this debris is unidentifiable, but *Permocalculus* spp., *Actinoporella podolica*, and *Salpingoporella arabica* can be recognized : their study was greatly facilitated by the occasional discovery of whole or near-complete segments, verticils or individual

thalli. *Munieria* is the most fragmentary of all : it survives as little looped or hooked scraps. These have been identified by reference to the figured random cuts of debris of Carozzi (1955a), supplemented by the figures of Radoičić (1959), rather than by comparison with Pia's topotype material (1920). Since the calcification of *Munieria* is proportionally heavier than that of the comparable *Actinoporella*, it is reasonable to suppose that in life it was more porous and hence more fragile when the skeleton was dismembered.

It seems not unlikely that the combined records of the various European and Middle East occurrences, Kimmeridgian to Albian, embrace more than one species: differences in average size and proportions, number of branches per verticil, etc. are suggested by the random thin-sections of various authors (e.g. compare the figures of Radoičić 1958 with those of Delmas & Deloffre 1962). Such a revision would have to be made on much better material than has been available for the present study : the Middle Eastern debris, therefore, is here referred to *M. baconica*, the only described species. The alleged figure of a complete verticil of a Middle East *Munieria* (Elliott 1958a, pl. 48, fig. 1) is an error.

Genus ***NEOMERIS*** Lamouroux 1816

DIAGNOSIS. Calcified tubular dasyclads showing successive verticils of branches in which each primary branch divides into a stalked sporangium and two secondary sterile branches set in the same plane : the calcification surrounds the sporangia and secondaries, but not the primaries, which are weakly calcified or uncalcified.

Neomeris cretacea Steinmann
(Pl. 15, figs. 1, 2)

1899 *Neomeris* (*Herouvalina*) *cretacea* Steinmann : 149, text-figs. 14–18.
1955 *Neomeris cretacea* Steinmann ; Elliott : 126, pl. 1, fig. 7.
1960 *Neomeris cretacea* Steinmann ; Elliott : 223.

DESCRIPTION (from Middle East material). Slightly irregular tubular calcified dasyclad of 1·10–1·25 external diameter, internal diameter 41–48% external, length (incomplete) seen to 6 mm. ; walls showing close-set verticils of neomerid groupings of sterile branches of about 0·050 mm. diameter and ovoid sporangia of 0·180 mm. length and 0·090 mm. diameter.

HORIZON. Upper Cretaceous of Mexico, Iraq and possibly from circum-Mediterranean ; top Albian of France (Delmas & Deloffre 1962).

MATERIAL. Two good sections only ; from the Bekhme Formation (Maestrichtian) of Chia Gara, and from the Aqra/Bekhme Limestone development (Campanian-Maestrichtian) of Gal-i-Mazurka at Amadia ; both localities in Mosul Liwa, Iraq. Numerous random thin-sections, completely or near-completely recrystallized, possibly of the same species, possibly of other species of this genus, occur in the Upper Cretaceous Limestones of Iraqi Kurdistan.

REMARKS. Steinmann's species was described from the Cenomanian of Mexico (Steinmann 1899). His specimens showed a larger size than the Iraqi material :

up to 2 mm. external diameter and an estimated length of 10 mm. Some of the indeterminable recrystallized Iraqi specimens reach this diameter. Dimensions of branches and sporangia are comparable in the two occurrences. Fragmentary Cretaceous material referred to the genus *Neomeris* has been described or recorded from the Danian of Morocco (Pia 1932), Cenomanian of Libya (Pia 1936a), Upper Cretaceous of Morocco (Pfender 1938) and Cenomanian–Turonian of Spain and Southern France (Pfender 1940). See also Massieux (1966b : 115, fig. 1).

Although the Iraqi evidence is very limited, it seems reasonable, in view of the measurements taken, especially of the sporangia, to refer the specimens to Steinmann's species. There is a resemblance between Pl. 14, fig. 2 of the present work and Steinmann's text-fig. 15, corresponding apparently to similar orientation of section and to individuals of similar development. If published dimensions and measurements on illustrations are combined, the Iraqi specimens are seen to be thicker-walled (d/D 41–48%) than the type-material (d/D 48–60%), but this is closer than the very thin-walled French Albian specimens (d/D 62–78%) of Delmas & Deloffre (1962), which should probably be referred to a new species, and which compare in this respect with the Lower Cretaceous *N. pfenderae* Konishi and Epis (1962). The difficulties of comparing species based on different kinds of fossil evidence (whole or fragmentary, few or numerous well-preserved specimens, etc.) are especially marked with Cretaceous *Neomeris*. It may be that further material would show the Iraqi form, which is Senonian-Maestrichtian, to be a different species from the type which is Cenomanian-Turonian, but it is closer to it than are the older species.

Genus ***PAGODAPORELLA*** Elliott 1956

DIAGNOSIS. Small calcified tubular dasyclad showing externally vertical rows of slightly alternating large pores with small interpore portions, the pores widening sharply from within outwards.

Pagodaporella wetzeli Elliott

(Pl. 17, figs. 9, 10)

1956 *Pagodaporella wetzeli* Elliott : 333, pl. 2, figs. 3, 4.

DESCRIPTION. Small tubular calcified dasyclad ; observed length (incomplete) 1 mm., external diameter about 0·34 mm., internal diameter 58–66% of external, octagonal in cross-section. Successive verticils of about eight branches each, 11–14 verticils per mm. of tube-length ; branches represented by large pores, externally roughly hexagonal and separated only by narrow interstices of calcareous wall-material : internal pore-diameter 0·040–0·050 mm., widening sharply to an extrenal diameter of 0·065–0·090 mm., so that in vertical section the wall-material shows as small well-spaced triangles or wedges, the apices outward. Externally the large window-like pores give an appearance of slightly irregular vertical rows.

HORIZON. Palaeocene–Lower Eocene of Iraqi Kurdistan.

MATERIAL. Solid and thin-section specimens from the Kolosh Formation

(Palaeocene) of Bekhme, Erbil Liwa ; thin-section material from the Sinjar Formation (Palaeocene–Lower Eocene) of Banik, Mosul Liwa, and from the Kolosh Formation (Palaeocene–Lower Eocene) of Sedelan, Sulemania Liwa ; all in northern Iraq.

REMARKS. *Pagodaporella* is the fossil record of a little, thick- branched dasyclad which calcified only near the stem-cell, at the base of the branches, no traces being left of branch-structure nor of sporangia : its relationships are therefore uncertain. The peculiar thin-section appearance, with more gaps than skeleton, was known for some time before the discovery of solid specimens, which when sectioned led to the elucidation of the random sections.

The living *Dasycladus* (*D. clavaeformis* (Roth) Ag. ; Mediterranean) shows a comparable limited calcification which is however not identical. Here each verticil shows 10–15 branches, branched outwardly to the third degree and also bearing sporangia : the primaries narrow markedly at their inner junctions with the stem-cell, and between their points of insertion the fleshy stem-cell wall is markedly thickened inwardly, within the stem-cell itself, and thinly calcified externally.

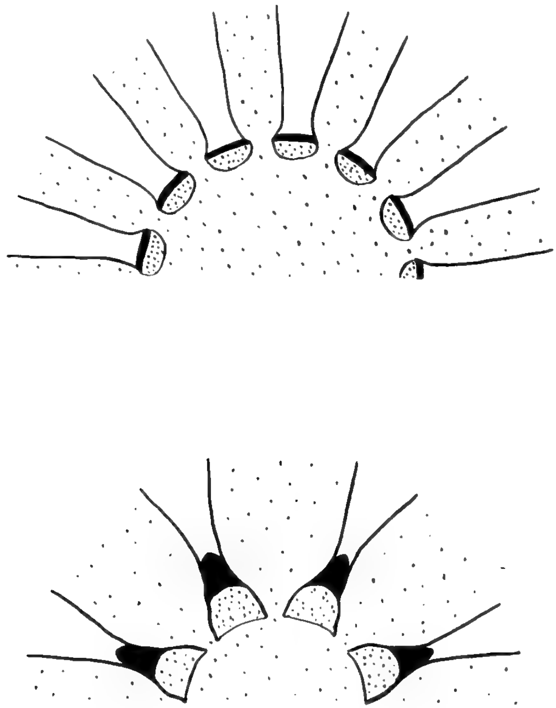


FIG. 4. Diagrammatic transverse sections of *Dasycladus* (above) and *Pagodaporella* (below, hypothetical). Greatly enlarged, ×150 approx. Spaced stipple, plant tissue ; close stipple, thickened portions of stem-cell wall ; black, calcareous structure. Each section shows half the stem-cell with branches attached. The reconstruction for *Pagodaporella* explains the possible origin of the structure found fossil.

(Fritsch 1935 : 388). If fossilized this structure would give a very thin cylindrical test perforated by alternating pores. If however calcification were to develop further outwards between the swelling primaries, wedge-shaped interstices would develop, but much closer than in *Pagodaporella*. Since dasyclad branches are normally thin at the points of origin and then swell out, it may be that *Pagodaporella* was like *Dasycladus* but with fewer, thicker branches, and that a thickened fleshy stem-cell wall bulged *outwardly* rather than inwardly between branches and was then calcified more heavily than in *Dasycladus*. (Fig. 4). If this were so the *Pagodaporella* skeleton would represent the calcification between swelling primaries, but separated from the level of their points of insertion by the thickness of the externally intermittently swollen stem-cell wall. In this way the present internal cavity of the fossil would be a record of the maximum diameters of the stem-cell, and the thin points of insertion of the primaries would have been some little distance inside the cavity.

Pagodaporella is therefore tentatively referred to the Dasycladeae : we know that branched choristospore laterals, seen in living genera of the tribe, had already evolved by the Palaeocene from the evidence of heavily calcified genera, e.g. *Cymopolia*. This structure may well have been present in *Pagodaporella*, even if no calcified evidence remains, and it may be that the genus is ancestral to the living *Dasycladus* : reduction of calcification and increase in number of branches seems a likely evolutionary trend.

Genus ***PALAEODASYCLADUS*** Pia 1927
(***PALAEOCLADUS*** Pia 1920 *non* Ettingshausen 1885)

Diagnosis. Elongate near-cylindrical club-shaped calcified dasyclad, showing numerous successive verticils of strongly-inclined branches : the branches show primaries, dividing into clusters of four to six secondaries, in turn dividing into clusters of four to six tertiaries. All branch-segments slightly swollen : successive verticils show a progressive elaboration of branch-detail.

Palaeodasycladus mediterraneus Pia
(Pl. 16)

1920 *Palaeocladus mediterraneus* Pia : 118, pl. 6, figs. 1–5 ; text-fig. 22.
1927 *Palaeodasycladus mediterraneus* Pia : *in* Hirmer's " Handbuch der Paläobotanik ", Bd.1 79.
1960 *Palaeodasycladus mediterraneus* Pia ; Elliott : 221.

Description (from Middle East material). Near-cylindrical elongate club-shaped dasyclad, length 7–8 mm. or more, external diameter increasing slowly and regularly from 1 mm. or a little less at the base to about 2·4 mm. in the terminal expansion, internal diameter from about 50% of corresponding external measurement at the base to about 30% or less at the terminal expansion *i.e.* the stem-cell cavity diameter increases only slowly compared to the external measurement. Close-set successive verticils of branches, 5 or 6 per mm. of measured length in mid-thallus : each verticil

with up to 20 branches, in which the primaries are inclined outwards and upwards at 45–50° from the horizontal, and the subsequent branchlets curve outwards at a lessening angle. Each primary gives rise to four or more secondaries, and these in turn to about the same number of tertiaries ; all branches and branchlets are sharply constricted terminally, slightly swollen between to give a slim sausage-shaped outline, and the tertiaries may themselves be constricted, without branching, before the final termination expansion. The branches from the lower verticils, at lesser diameters, are simpler in structure than the much larger terminal ones : the transition is gradual.

HORIZON. Lias of Southern Europe, North Africa and the Middle East.

MATERIAL. Numerous random thin-sections from one level in the median dolomitic limestone of Group *a* (Liassic) of the Lower Musandam Limestone ; Wady Bih, Jebel Hagab, Peninsular Oman (Hudson & Chatton 1959).

REMARKS. *Palaeodasycladus mediterraneus* is a characteristic and locally-

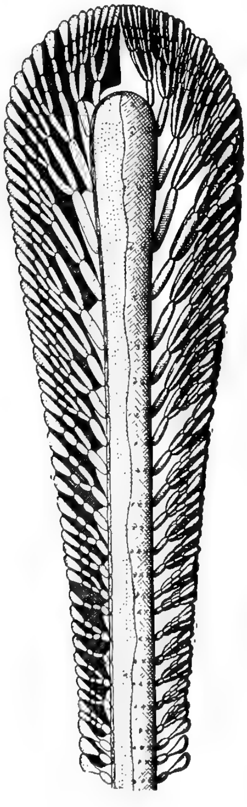


FIG. 5. Reconstruction (after Pia 1920) of *Palaeodasycladus mediterraneus* Pia. Vertical section on left ; decalcified appearance on right. ×12 approx.

abundant microfossil in the Lias of the circum-Mediterranean area, namely Spain, Italy, Greece, Morocco and Algeria. Its total range appears to be from within the upper part of the Lower Lias, through the Middle Lias, and into the lower part of the Upper Lias ; there are records from top Triassic which need confirmation (Sartoni & Crescenti 1962). The usual associated microfossil is the foraminifer *Orbitopsella praecursor* (Gümbel). In the Middle East *P. mediterraneus* is known to me only from Oman, where it is locally abundant in one bed of the Dolomitic Limestone of the Lower Musandam, associated with algal nodules, and probably of Middle Liassic age (see Hudson & Chatton 1959 : 78). *Orbitopsella* is known from S.W. Persia, but I have not seen *Palaeodasycladus* associated in this limestone, though it is likely to occur there. A. Gollestaneh has, however, recently discovered this dasyclad in the lower to middle Lias of Khaneh Kat, interior Fars province. It is interesting that in Oman, *Orbitopsella* occurred more or less throughout the Liassic rocks, whilst *Palaeodasycladus* was restricted to one bed : in southern Italy, however, the alga has a much greater vertical range than the foraminifer (Sartoni & Crescenti, 1962 ; de Castro 1962).

P. cf. *mediterraneus* from the subsurface Jurassic of Haifa, Israel, is Middle Jurassic in age (Maync, 1966 ; Derin & Reiss 1966).

In general, the Oman material confirms the accuracy of Pia's original reconstruction of *Palaeodasycladus* (Pia 1920 : 121). Sizes reached are less than those of large Italian specimens, for which 12 mm. length and 2·8 mm. maximum external diameter are quoted (Sartoni & Crescenti 1960 : 14). Although the dolomitised nature of the Oman specimens is not ideal for elucidation of fine detail, there appear to be several small differences. The ragged outline of the stem-cell cavity, clearly figured by Pia and ascribed by him to incomplete inner calcification on alternate verticils, was only seen on one incomplete example, where it may well be due to the dolomitisation of the stem-cell filling. The branches, although constricted as figured by Pia, appeared less swollen and slimmer than in his reconstruction, and although constriction of tertiaries without branching does occur, it was much less marked than in his figures. Finally Pia's reconstructed successive cross-sections (*op. cit.* : 121), show a reduction in the number of branches per verticil, from base to apex, 18 to 12, so accommodating the increased branch-complexity. In the Oman material this is much less obvious, if it occurs at all, and although counts of branching are difficult on sections of this crowded, highly-oblique, structure, about 20 branches have been counted at a large verticil. This is apparently to be correlated with the thinner branches already noted. It is suggested that *Palaeodasycladus* retains the number of branches per verticil during growth, or even increases them slightly like many other dasyclads, and that the reduction seen in Pia's admirable clear figures is a cartographic necessity rather than an accurate depiction.

The Oman material is referred here to *P. mediterraneus*, and there is no reason to make it a new species or variety. It is not comparable with the distinctive *P. mediterraneus elongatulus* (Praturlon 1966).

The modern appearance of *Palaeodasycladus* is striking when compared with some of Pia's other bizarre reconstructions from the Mesozoic. Probably the spores were

borne in the swollen branches. It is easy to see how such an alga, with development of separate reproductive bodies, would resemble certain living genera, e.g. *Dasycladus* itself, allowing for the very different calcification.

The Oman *Palaeodasycladus*-limestone is crowded with examples of the species : presumably they grew in dense patches or thickets like the living *Dasycladus*. Their ecology is further discussed below.

Genus ***PERMOPERPLEXELLA*** gen. nov.

DIAGNOSIS. Thin hollow calcified elongate claviform dasyclad ; walls showing consecutive horizontal verticils of large cylindrical branches, rounded in cross-section, pores (branches) of adjacent verticils set alternately, all pores separated by narrow interstices ; proximal and distal terminal openings to thallus.

HORIZON. Permian of Iraq.

TYPE SPECIES. *Permoplexella attenuata* sp. nov.

Permoperplexella attenuata sp. nov.

(Pl. 17, figs. 1–5)

DESCRIPTION. Hollow elongate calcified club-shaped thallus, length about 2·5 mm., external diameter increasing gradually from 0·5 mm. near the base and swelling to 0·9 mm. or more sub-terminally, internal diameters 45–46% external, ends rounded, terminal apertures of about 0·156 mm. and 0·312 mm. diameter respectively. About 22 consecutive verticils each of about 20 branches, branches in successive verticils arranged alternately. The branches in vertical section are seen to communicate with the internal cavity by a narrow pore, and expand at once to a rounded rectangular section, occasionally seen as flask-shaped in the terminal expansion of the thallus. In cross-section they are rounded-polygonal, about 0·1 mm. diameter, and separated by calcareous interstices of 0·020 mm. or less. Traces of a narrow longitudinal calcified structure within the central cavity.

HORIZON. Permian of Iraqi Kurdistan.

HOLOTYPE. The specimen figured in Pl. 17 fig. 4, from the Permian Zinnar Formation ; Ora, Mosul Liwa, Iraq. V. 52085.

PARATYPES. The specimens figured in pl. 13 figs. 1–3, 5 ; same locality and horizon. V. 52084, 52085.

OTHER MATERIAL. Random sections in the same samples.

REMARKS. The little dasyclad described above, although distinctive enough in the Iraqi Permian flora studied, shows a combination of characters which are not themselves intrinsically distinctive. The pores (side-branches of the verticils) are simple and do not consistently show any of the shapes characteristic of the different genera of the diploporeae—*Diplopora, Gyroporella, Physoporella,* etc. Although the thallus is that of the conventional single dasyclad, the terminal apertures suggest that it may possibly be a unit of a serial plant ; for whilst it is true that in some of the more elaborate dasyclads of later geological periods the distal aperture is occupied

by a tuft of narrow sterile branches, we do not know whether these simple-branched late Palaeozoic dasyclads were similar in this respect. The fossil is presumably not to be regarded as a new small species of *Eogoniolina* Endo, which has no distal aperture ; its branches are not those of *Gyroporella*, and it is smaller and with different shaped thallus than the somewhat doubtful *Pseudogyroporella* (Endo 1959). Although segments of *Mizzia* spp. auct. vary considerably, the fossil under discussion is outside the known range of segment-shape for this genus. It is moreover rare amongst an abundance of *Mizzia*, and the calcareous traces in the stem-cell cavity, never seen in any of very many *Mizzia*-segments examined, suggest a different internal organisation. It seems best to admit that its exact place amongst the dasyclads is at present obscure, and to describe it as a new genus, tentatively referable to the tribe Diploporeae.

Genus ***PIANELLA*** Radoičić 1962

DIAGNOSIS. Calcified cylindrical dasyclad tube showing successive verticils of horizontally directed branches, alternating in position from one whorl to the next : branches simple, unbranched, widening evenly outwards from a narrow insertion at the stem-cell cavity to the anterior : i.e. differing only from *Macroporella* in the regular verticillate, instead of irregular, insertion of the branches at the stem-cell.

Pianella gigantea (Carozzi) Radoičić

1955a *Macroporella gigantea* Carozzi : 43, pl. 6, fig. 4 ; text-fig. 7.
1960 *Macroporella gigantea* Carozzi ; Elliott : 221.
1962 *Pianella gigantea* (Carozzi) Radoičić ; Radoičić : 202.

DESCRIPTION (based on Carozzi). Calcified cylindrical dasyclad tube of 1·2–1·75 mm. external diameter, internal diameter 66–70% of corresponding external diameter; successive verticils of horizontally directed branches, 30–40 per verticil, widening from 0·03 mm. diameter internally to 0·09–0·20 mm. externally to give a regular external pattern of polygonal pores.

HORIZON. Upper Jurassic of Europe (Switzerland) and Arabia (Oman, Hadhramaut).

MATERIAL. Upper Jurassic of Jebel Kaur, Oman ; also in derived Upper Jurassic in the Upper Cretaceous Hawasina-complex at Jebel Buwaida, Ibri, Oman. Fragmentary remains in Upper Jurassic of the Jebel Laut area, Wahidi State, Hadhramaut, and see also Hadhramaut record of Beydoun (1960 : 140).

REMARKS. Carozzi described his species from the Sequanian-Portlandian of the Swiss Upper Jurassic. Associated fossils and stratigraphy suggest the upper part of the Upper Jurassic for the Middle East occurrences also. The species is apparently uncommon there and remains are fragmentary or poorly preserved. Praturlon (1966) relegates this species as a synonym of *P. pygmaea* (large individuals).

Pianella pygmaea (Gümbel) Radoičić
(Pl. 17, figs. 6–8)

1891 *Gyroporella pygmaea* Gümbel : 306, text-figs. 6, 7.
1924 *Macroporella pygmaea* Gümbel spec. ; Pia : 84, pl. 1, figs. 4–7.
1955a *Macroporella pygmaea* Gümbel ; Carozzi : 40, pl. 6, fig. 3 ; text-figs. 5, 6.
1960 *Macroporella pygmaea* (Gümbel) ; Elliott : 222.
1962 *Pianella pygmaea* (Gümb.) Rad. ; R. Radoičić : 202.

Description. Calcified cylindrical dasyclad tube, external diameter 0·33–0·78 mm., internal diameter 0·10–0·34 mm. (d/D 27–43%, usually about 30%), showing consecutive horizontal verticils of branches, about 18–20 verticils per mm. of length, each verticil of 15–20 branches. The branches are straight, unbranched, near-circular in cross-section, and widen radially with straight sides to the exterior, from a very narrow insertion on the stem-cell cavity to the exterior where they have a diameter of about 0·052 mm., sometimes with a terminal widening to give a diameter of 0·090 mm.

Horizon. Upper Jurassic to bottom Cretaceous (Sequanian–Valanginian) of Central and Southern Europe (Switzerland, Italy, Southern Germany), Middle East and Borneo.

Material. In the Middle East, from the Garagu Formation (Valanginian), subsurface at Awasil no. 5 well and Mileh Tharther no. 1 well, both Dulaim Liwa, Iraq. Also from the Upper Jurassic of the Jebel Laut area, Wahidi State, Hadhramaut, and see Hadhramaut record of Beydoun (1960 : 140).

Remarks. *P. pygmaea* from the Middle East is closely comparable in dimensions and structure with the European material described by Pia and by Carozzi (ref. Carozzi 1955a). The external diameter of the pores is usually less (0·05 mm. compared with 0·09 mm.), though not invariably so. Of comparable species, *P. grudii* Radoičić, from the Kimmeridgian of Jugoslavia, is a smaller species with proportionally wider stem-cell ; *P. tosaensis* Yabe & Toyama, from the Upper Jurassic of Japan, shows about 30 branches per verticil, and these are polygonal in cross-section, with expanded outer terminations.

Genus ***PSEUDOEPIMASTOPORA*** Endo 1961

Diagnosis (after Endo). Thallus short-elliptical, somewhat undulating, almost circular in cross-section ; branches widening within the wall-thickness to spherical cavities (believed sporangial) and narrowing again, set at right angles and slightly ascending to the vertical axis, and may be arranged as definite verticils.

Pseudoepimastopora was instituted by Endo (1961) to include those species of the older genus *Epimastopora* s.l. in which the pores seen penetrating the walls swell from a narrow entry to a more or less globular cavity within the wall-thickness and constrict again : these swellings were considered sporangial in origin. This left *Epimastopora* s.str. for species in which the pores traverse most of the wall thickness with little change in pore-diameter. Buri (1965) does not regard this division as significant, or of generic value. I agree that it may not be evidence of evolutionary

divergence, but it forms a useful character at present in classifying these normally fragmentary and rather unsatisfactory dasyclads. Both these genera are normally represented almost entirely by wall-fragments : straight, curved or sinuous in section, and they are considered to be the broken remains of the very fragile thin hood-like outer calcification-zone of dasyclads whose stem-cell and branch-systems are necessarily unknown. A comparison has been made with the Carboniferous *Koninckopora* as restored by Wood (1943), who regarded them as very closely related. However the outer polygonal mesh of *Koninckopora* is very different in appearance to the pored walls of *Epimastopora* and *Pseudoepimastopora*, even if all three are representatives of a morphologically similarly-situated outer calcification-zone.

The fragmentary remains of the latter two genera have led to a proliferation of species based on wall- and pore-measurements (see summary in Johnson 1963). The calcified structures themselves have usually been reconstructed as originally globular or tubular. Endo (1961) cited *P. pertusus* as type-species, and referred his earlier *E. japonica* also to the genus. Subsequently H. Flügel (1963) has transferred both *E. likana* Kochansky & Herak and *E. iwaizakiensis* Endo (Permian of Jugoslavia and Japan respectively), to *Pseudoepimastopora*, figuring both from the Middle East. *P. iwaizakiensis*, from the Taurus (Southern Turkey) Permian of which the Iraqi Kurdistan Permian is a continuation, is shown intact in presumably near-longitudinal section as a very thin-walled elongate-oval. (H. Flügel 1963).

Remains of *Pseudoepimastopora*, usually fragmentary, abound in the Zinnar Formation, the lower portion of the Chia Zairi or Iraqi Permian System. Fortunately one or two whole specimens have been seen, so permitting description of a distinctive new species.

Pseudoepimastopora ampullacea sp. nov.

(Pl. 18, figs. 1, 2, 5–7)

Description. *Pseudeopimastopora* of " waxing-and-waning " morphology, circular in cross-section, length about 4·0 mm., diameters (three successive maxima) 1·56, 1·43, 0·91 mm. : thin-walled, wall-thickness 0·078–0·104 mm., pores commencing on the inside as narrow canals, and swelling within the wall-thickness to near-spherical cavities of 0·052–0·065 mm. diameter, with outer opening of varying size, commonly about half maximum diameter ; interpore spaces (solid wall) very narrow so that there are about 16 pores per 1 mm. of wall-length, outer apertures of pores believed to be close-set in alternating levels.

Horizon. Permian of northern Iraq.

Holotype. The specimen figured in Pl. 18, fig. 1 from the Permian Zinnar Formation, Ora, Mosul Liwa, Iraq. V. 52089.

Paratypes. The specimens figured in Pl. 18, figs. 2, 7, Zinnar Formation, Ora and Harur, Mosul Liwa, Iraq. V. 52090, 52094.

Other Material. Numerous random thin-sections : many specimens fragmentary. Same formation and area.

REMARKS. This species occurs in profusion in some samples as debris ; short curved pieces of wall showing the pore-structure. These random cuts are commonly at right angles to the wall and show the near-spherical cavities well ; other, tangential, cuts may show the inner narrow initial canals, or the arrangement of larger external pore-openings. Larger pieces of wall showing much curvature are relatively uncommon, and near-complete specimens are very rare. The holotype is a longitudinal section showing two complete diameter-maxima and a third slightly crushed: detail not seen on this specimen is well-displayed by debris in the same thin-section.

P. ampullacea differs in its distinctively lesser wall-thickness and rather smaller pore-diameter from *P. pertunda* Endo (type), *P. japonica* Endo and *P. iwaizakiensis* Endo. Also from the coarser *P. likana* Kochansky & Herak, known from elsewhere in the Middle East (see below). In outline *P. ampullacea* is distinctive, though Endo's description of the thallus of his fragmentary *P. pertunda* and *japonica* as " somewhat undulating " may indicate a similar growth-form.

Pseudoepimastopora cf. ***likana*** Kochansky & Herak
(Pl. 18, figs. 3, 4)

1960 *Epimastopora likana* Kochansky and Herak : 78, pl. 4, figs. 5–10.
1960 *Epimastopora* sp. Elliott : 219.

Fragments of *Pseudoepimastopora* occurring in the Permian of Jebel Qamar, Oman, show a wall-section of 0·325 mm. thickness, with well defined ovoid pores of 0·130 mm. median diameter in vertical section. In this section the pores appear oval with pointed ends, communicating with the interior by a short very narrow canal, and with the exterior by an even shorter one. They are close-set, though this feature varies in the limited material available.

This species corresponds most closely to *Ps. likana* but the dimensions seem larger. In the type-material of the Yugoslav species the wall diameter is given as 0·20–30 mm. (most frequently 0·25 and the pore-diameter maximum 0·07–0·10 mm. (misprinted as 0·7–0·10 mm.). The Oman material is insufficient to be described as new.

The specimens occurred in thin-sections of limestone boulders yielding *Anthrocoporella mercurii* sp. nov. *Pseudoepimastopora* fragments have also been seen in derived Permian material in the Lower Cretaceous Upper Musandam formation of Jebel Hagab in the same areas.

Pseudoepimastopora iwaizakiensis Endo

1953a *Epimastopora iwaizakiensis* Endo : 120, pl. 11, figs. 7–9.
1963 *Pseudoepimastopora iwaizakiensis* (Endo) ; Flügel : 88, pl. 1, fig. 6.

Figured by Flugel (1963) from the Permian of the Taurus, Turkey.

Genus ***PSEUDOVERMIPORELLA*** Elliott 1958

DIAGNOSIS (after Elliott). " Small gregarious meandriform calcareous tubes, showing a free inner compact-walled tube and an outer tubular layer that is pierced by numerous closely set radial pores arranged to form a regular mesh ".

Pseudovermiporella was described by me in some detail (Elliott 1958b) as a Permian problematicum, and an algal interpretation given of its structure. Kochansky & Herak (1960), in discussing Permian *Vermiporella* spp., agree as to the algal nature of *Pseudovermiporella*, but consider that it is not worthy of generic distinction from *Vermiporella*, and that the details described should be considered a " contribution to the knowledge of the genus *Vermiporella* ". Henbest (1963) regards *Pseudovermiporella* as a foraminifer : " A specialized, sessile form of Permian Cornuspirinae " whose originally aragonitic test has undergone a distinctive diagenetic change.

These three views depend on the interpretations made of the structure and preservation of a very distinctive microfossil.

My account (Elliott 1958b : 420) briefly discussed and discounted the possible interpretations of *Pseudovermiporella* as a foraminifer, bryozoan, serpulid, dasyclad alga of conventional structure, or hemichordate. My suggested interpretation of the problematic fossil regards the outer mesh as the main calcified layer of a dasyclad of creeping or prostrate stem-cell, perforated around lateral branches, as in *Vermiporella*. The variable inner layer or layers of grey calcite lining this in the type-material are regarded as a secondary deposit, not part of the organism, formed after death and before burial. The very distinctive thin imperforate tube found in some but not all specimens, within the main cavity of the outer mesh-tube, is considered the calcified outer surface of the early stem-cell, after the side-branches dropped off, behind the actively growing anterior branched portion.

Kochansky & Herak (1960) described Jugoslav Permian species of *Vermiporella*, including *V. nipponica* Endo, a Japanese species to which *Pseudovermiporella* was compared by me. *Vermiporella* itself has a Silurian type-species, *V. fragilis* Stolley, whose dasycladacean nature has not been disputed. There has been, however, considerable confusion over poorly-described Permian species referred to the genus, and Kochansky & Herak dealt with this. They did not record *Pseudovermiporella* (or *Vermiporella*) *sodalica* in their material, but concluded (*op. cit.* : 72–73) that the main difference between four recognized species of *Vermiporella* (including the type) and *Pseudovermiporella* is the presence of the " free inner compact-walled tube " in the latter. They quoted me correctly as not having seen this structure in all examples, and regarded this as growth-stage detail in a very full description of a species of *Vermiporella* not worthy of generic distinction.

Henbest (1963 : 33) interprets *Pseudovermiporella* as a " specialized, sessile genus of Permian Cornuspirinae " continuing a series formed by the earlier genera *Apterrinella* and *Hedraites*, with which he compares it closely. All three are interpreted as originally aragonitic foraminifera which have undergone conspicuous changes during diagenesis : it is important that in this interpretation the inner layers of grey calcite lining the outer mesh are regarded as an integral part of the test itself. In correspondence, after examining topotype material sent by me (letter of August 17, 1964) Henbest regards the free inner thin-walled tube as that of " a later individual or organism ".

The three accounts quoted should be read for a full appreciation of the differing

interpretations of various minor points and comparisons : it is, however, believed that the summary above includes the essential differences.

I described *Pseudovermiporella* as a problematicum, probably algal, and believe that the presence of the inner thin-walled tube is important. It is not recorded in Permian *Vermiporella* spp. elsewhere, and although it is not seen in all specimens, its occasional presence unbroken and set in clear calcite free of the outer structures suggests that it was part of the organism and not a later inhabitant of the abandoned tube. It is, however, readily admitted that the exact nature of *Pseudovermiporella* remains unknown : its description is included here as a doubtful dasyclad of the Middle East. Güvenç (1965), who figures un-named species or forms from the Taurus, leaves it as a problematicum. The microproblematicum *Papillomembrana* from the Norwegian Precambrian (Spjeldnaes 1963) bears certain resemblances, from the type-description.

NOTE. The interesting study by K. B. Korde (Pal. Zhurn., 1966 no. 4) was seen too late for proper discussion here, but briefly this authoress agrees with the probable algal nature of *Pseudovermiporella*, whilst unable to place it taxonomically within the algae.

Pseudovermiporella sodalica Elliott

(Pl. 19)

1958b *Pseudovermiporella sodalica* Elliott : 419, pls. 1, 2, 3.
1960 *Pseudovermiporella sodalica* Elliott ; Elliott : 219.
1961 *Pseudovermiporella sodalica* Elliott ; Erk & Bilgütay ; 108, pl. 1.

DESCRIPTION. Tubes of finely crystalline calcite, appearing white by reflected light and dark in thin section, occurring commonly with various diameters up to 1·0 mm. and sometimes attaining a diameter of 1·4 mm. The tubes are meandriform and form tangled growths several millimeters across, in which apparently more than one individual may occur. When a tube is free the cross section is circular, and remains approximately so in many coils or loops, which touch in a growth or tangle. However, when attached to others or to shell fragments, individuals occur which show in thin section as arcs applied closely to the object encrusted, whose outer surface completes the tube.

The tubes are pierced by numerous closely set radial pores, approximately at right angles to the axis of the tube, separated by interpore wall material which widens slightly outward, or terminally, as seen in transverse and vertical sections. In adult individuals the pores are about 0·030–0·040 mm. in diameter, circular in cross section, about fifty to a transverse section of the tube, and the interpores of wall material sometimes show a paired appearance in both transverse and vertical section. In tangential sections the coarsely-pored wall shows as a regular and distinctive round-pored mesh, with pores wider than interpores ; a count along a 1 mm. length of such a section gave twenty-one regularly spaced pores. Such measurements are approximate only, due to the coiled tubes, which are at best only sinuous and never straight. Smaller tubes show smaller pores.

Within the outer pored tube described above there occurs in a majority of specimens a continuous solid dark calcareous layer, attached to the inner surface of the outer mesh. In many specimens this layer is indistinguishable in colour and texture from the dark outer calcite mesh, and has the appearance of being part of the tube ; in some it shows as a lighter, obscurely banded layer of variable thickness, eccentrically placed with regard to the outer tube, i.e. much thicker on one side than on the other in transverse section ; and sometimes it is absent. This layer is interpreted as a secondary deposit formed subsequent to the death of the tube-building organism, though not after burial, for occasional specimens show other organisms attached to its inner surface. The reason for its occurrence is discussed above. Consideration of the algal dust infillings described in *Koninckopora* by Wood (1943) did not permit close comparison, but the observations of Johnson (1957 : 181) are of interest. The lining layers in *Pseudovermiporella* may be of similar origin to the granular crystalline calcite described by Johnson, and considered by him to have been formed probably almost contemporaneously with deposition, whilst objects were movable on the sea-floor.

Within some but not all specimens there occurs an innermost tube of thin dark imperforate calcite, roughly circular in cross section, and of considerably lesser diameter than the inner diameter of the outer tube from mesh to mesh. Sometimes this thin layer forms the inner boundary of the secondary layer mentioned above ; sometimes it is seen " free " within the central cavity, filled with transparent calcite and separated by the same mineral from the outer pored tube or from the dark secondary lining calcite if present. When intact, it is not invariably central in position ; not infrequently it is broken, and sometimes small organisms are seen attached to it. It is considered to be of organic origin, and its relation to the outer pored tube is discussed above.

The smallest tubes show in section as bubble-like clusters, rather like the nucleoconchs of certain foraminifera. Although some of the sections in such a cluster are a result of the plane of section cutting a meandriform tube more than once, it seems likely that more than one individual, budding from a centre, may sometimes be present. The walls of these tiny immature tubes are composed of the innermost thin dark organic calcite just described ; only when they are larger does a pored outer tube, with proportionally small pores, appear. There is considerable variation between individuals in the diameter-size at which this occurs.

In sections of the mesh of adult individuals, small bubble-like sections of the inner layer of small, usually single individuals sometimes occur, suggesting attachment or budding. Small pored tubes occur within the tubular cavities of larger individuals, attached either to the inside of the main outer mesh (rarely to the secondary calcite lining this, if present) ; or to the outside of the inner, thin-walled tube. They are never found within the latter when it is unbroken.

HORIZON. Upper Permian of the Middle East.

MATERIAL. Very numerous thin-sections from Permian limestone at Jebel Qamar, Peninsular Oman, Arabia (foraminiferally dated as probably Upper Permian by Dr. M. C. Chatton). Seen also in derived Permian material in Upper Cretaceous,

Tawi Silaim, Oman. In Iraq this species (or a comparable species of *Vermiporella*) occurs rarely in the Upper Permian Darari Formation of Harur, and in the subsurface Upper Permian of Atshan no. 1 well, both in Mosul Liwa. Recorded by Erk & Bilgütay (1961) from the Permian of Sarikaya, Diskaya Mountains, near Bursa, and from the Adana Basin, Turkey.

REMARKS. See discussion under " Genus *Pseudovermiporella* " above.

Pseudovermiporella elliotti Erk & Bilgütay

1961 *Pseudovermiporella elliotti* Erk and Bilgütay : 110, pl. 2.

REMARKS. This species appears similar in many characteristics and in mode of growth to the type-species. It differs, however, in the following points, summarized from the authors' description and comparisons. It is a smaller species (external diameter up to 0·539 mm.), the pores are hexagonal, not rounded in cross-section and both smaller in diameter (0·025–0·030 mm.) and more closely set (interpores of 0·010–0·013 mm. thickness). The individuals are said to occur singly, and not tangled or closely associated as in *P. sodalica*. It is not clearly stated whether an inner thin-walled tube occurs, though small individuals occur within larger ones, as in the larger species. It is recorded from the Turkish Permian at Kozan, Adana Basin and from various localities near Ankara. In the Adana area the two species occur commonly in rocks of Middle Permian age.

Genus ***SALPINGOPORELLA*** Pia 1918

DIAGNOSIS. Small, rod-like, thick-walled, calcified, tubular dasyclad, with regular successive verticils of relatively few simple single branches which widen to the exterior and open as simple pores : thallus not segmented, but interverticil portions sometimes outwardly slightly convex and delimited by grooves.

Salpingoporella annulata Carozzi

(Pl. 20, figs. 3, 4, 6, 7)

1953 *Salpingoporella annulata* Carozzi ; 384, figs. 1–55.
1955b *Salpingoporella annulata* Carozzi ; Elliott : 125, 126.
1955a *Salpingoporella annulata* Carozzi ; Carozzi : 55, pl. 6, figs. 5–7, text-fig. 15.
1960 *Salpingoporella annulata* Carozzi ; Elliott : 221.

DESCRIPTION (based on Carozzi). Small, tubular, calcified dasyclad, straight or slightly curved and usually occurring in fragments of up to 1 mm. or more in length, external diameter 0·30–0·64 mm., internal diameter 0·10–0·25 mm. The thick walls perforated by horizontal verticils of branches at about 0·15–0·20 mm. apart, each verticil consisting of 8–12 simple straight radial branches which widen terminally and open in a shallow external horizontal annular groove. Pores alternate in position from one verticil to the next, and between them the external interverticil walls are gently convex.

HORIZON. Upper Jurassic–bottom Cretaceous (Kimmeridgian, Portlandian-Valanginian) of Switzerland and Southern France, Italy, Jugoslavia : and of Middle East (Arabia) ; Qatar, Trucial Oman and Hadhramaut.

MATERIAL. Solid and thin-section material from the subsurface Upper Jurassic (upper part) of the Dukhan wells, Qatar Peninsula, Arabia, where it is common ; also at the same level in Gezira no. 1 well, Murban, Abu Dhabi, Trucial Oman. Also from the Upper Jurassic of Al Hamiah, Coastal Wahidi, Hadhramaut ; and from the subsurface Lower Thamama formation (bottom Cretaceous) of Murban no. 2 well, Abu Dhabi, Trucial Oman.

REMARKS. The Qatar material corresponds with Carozzi's type material in detailed morphology, number of branches per verticil, etc. : the maximum size seen (external diameter 0·60) is a little less than Carozzi records, and the minimum measurement encountered for this dimension (0·26 mm.) is also less than that given for the type-material. Since the closely similar *S. apenninica* Sartoni and Crescenti (see below) differs mostly in its smaller size, a series of Qatar specimens were carefully measured for outer and inner diameter and spacing between verticils. Of thirteen such examples, only one fell completely within the limits given for the smaller species, and it is considered that this is best regarded as a small example of *S. annulata*. At Qatar the material consists of short lengths only of tube, occurring amongst ooliths and rounded fragments and often rolled, and it may be that sorting has occurred before burial.

Salpingoporella apenninica Sartoni & Crescenti

(Pl. 20, figs. 1, 2, 5)

1962 *Salpingoporella apenninica* Sartoni and Crescenti : 266, pl. 44, figs. 1, 2, 4, 5, 6, 8.

DESCRIPTION (based on Sartoni & Crescenti). Small tubular calcified dasyclad, straight or slightly curved and usually occurring in fragments of up to 1 mm. or more in length, external diameter 0·19–0·32 mm., internal diameter 0·097–0·22 mm., the walls perforated by horizontal verticils of branches at about 0·08–0·16 mm. apart, each verticil consisting of 8–14 simple radial branches widening terminally and opening in a shallow horizontal annular groove. Pores alternate in position from one verticil to the next, and between them the external interverticil walls are gently convex.

HORIZON. Upper Jurassic–bottom Cretaceous (Kimmeridgian, Portlandian–Valanginian) of Italy : Upper Jurassic of Iraq.

MATERIAL. Abundant thin-sections from the subsurface Najmah Formation (Upper Jurassic) of Kirkuk no. 117 well ; also rarely in the subsurface Jurassic of Mileh Tharthar no. 1 well, Dulaim Liwa, believed to be a caving from the Makhul Formation (Tithonian) in this well. Both localities are in northern Iraq.

REMARKS. The Iraqi material corresponds well in morphology and dimensions with the Italian type-material (external diameters of 0·208–0·286 mm., internal diameters of 0·104–0·130 mm.). This species is very similar to *S. annulata* : the

principal difference in thin-section is that whilst the stem-cell diameters are slightly less in *S. apenninica*, the external diameters are much less, so that the percentage relation of internal to external is greater (50–60% against 33–40%). In *S. annulata* the distance between the external pores of the same verticil is said to be about equal to the distance between two successive verticils (Carozzi 1955a) ; in *S. apenninica* the former is less than the latter. The two species are very similar and obviously closely related : in examining a series of either one finds atypical specimens showing measurements more usual in the other species. In Italy they occur together over the same range : in the Middle East they are apparently separate, *S. annulata* in the south at Qatar and elsewhere, and *S. apenninica* in the north in Iraq. Both these occurrences are often in a similar oolitic facies, with associated fossils in common (*Clypeina jurassica, Favreina salevensis, Cladocoropsis*, etc.).

Salpingoporella arabica sp. nov.

(Pl. 21, figs. 1–3)

1955b *Salpingoporella* cf. *mühlbergii* (Lorenz) ; Elliott : 126.
1960 *Salpingoporella mühlbergi* (Lorenz), and *S. mühlbergi* var ; Elliott : 222–224.

DESCRIPTION. Thin-walled tubular calcified dasyclad, straight-sided with very gentle increase in diameter ; observed lengths (incomplete) up to 2·73 mm., external diameter 0·31–0·73 mm., internal diameter 0·21–0·47 mm. ; ratio of internal to external diameters 55–66% ; horizontal verticils set regularly 0·104 mm. apart, each verticil with 8–10 branches which open rapidly and widely to external pore-depressions of 0·065–0·078 mm. or more diameter. The wall calcification is thin and rather ragged : the pores have a somewhat irregular appearance, partly due to the wall-structure and partly due to slight irregular deviations from the horizontal in their orientation.

HORIZON. Lower Cretaceous of the Middle East.

HOLOTYPE. The specimen figured in Pl. 21, fig. 3, from the Qamchuqa Formation (Aptian-Albian level) of Surdash, Sulemania Liwa, Iraq. V. 52102.

PARATYPES. The specimens figured in Pl. 21, figs. 1, 2, from the top Qamchuqa Formation (Albian level) of Sarmord, Sulemania Liwa, Iraq, and from the Upper Musandam Formation (Lower Cretaceous) of Jebel Hagab, Peninsular Oman, Arabia. V. 52100, 52101.

OTHER MATERIAL. In Iraq, Qamchuqa Formation of Zibar-Isumeran, Mosul Liwa (Barremian-Aptian level) ; Sarmord Formation of Jebel Gara, Mosul Liwa (Valanginian-Hauterivian) and of Sarmord, Sulemania Liwa (Barremian). In Arabia, from Haushi, South Oman, Lower Cretaceous probably Valanginian-Hauterivian ; also from subsurface Upper Thamama Formation, ?Barremian-Aptian level, of Murban no. 2 well, Abu Dhabi, Trucial Oman.

REMARKS. *S. arabica* is the Middle East form of the European *S. mühlbergii* (Lorenz) Pia, with which I earlier tentatively identified it. The European species from the Barremian-Aptian of France and Switzerland and the Lower Cretaceous of

Italy (Lorenz 1902 ; Pia 1918, 1920 ; Thieuloy 1959 ; Sartoni & Crescenti 1962), is a slightly smaller species normally (external diameter 0·3–0·5 mm.), though Thieuloy's figures appear to indicate up to 1·5 mm. for this dimension. It is however much thicker-walled, the relation of internal to external diameters being about 40% (38–45%) as against 60% (55–66%) in *S. arabica*. Because of this, the branches in the latter rarely show much of the inner narrower portion seen in the European form, if indeed this was ever present. *S. texana* from the Albian of U.S.A. (Johnson 1965), compared by its author with *S. mühlbergii*, may similarly be distinguished from *S. arabica* by dimensions and proportions.

S. arabica ranges from bottom Cretaceous as high as Albian ; it is wide-spread, but rarely abundant.

Salpingoporella dinarica Radoičić

(Pl. 21, fig. 4 ; Pl. 22)

1959 *Salpingoporella dinarica* Radoičić : 33, pls. 3–5.
1960 *Hensonella cylindrica* Elliott : 229, pl. 8, fig. 1.

The descriptions of Radoičić (1959) and myself (Elliott 1960) refer to the same organism. Radoičić interprets this as an alga, and described it as a species of *Salpingoporella*, comparing it carefully with *S. mühlbergii* of the same age. I described it as a problematicum, since my interpretation of the wall-structure indicated that it differed very considerably from other dasyclads.

This organism is Tethyan Lower Cretaceous in age, and is especially characteristic of the Barremian-Aptian level. The type-description of *S. dinarica* lists it from numerous localities in Jugoslavia at this horizon, and Sartoni & Crescenti (1962) and de Castro (1963) figure and record it under the algal name, with *Hensonella* in synonymy, from the Aptian of Italy. Elliott (1960 ; 1962a) recorded *Hensonella* from Iraq and Oman (a full list of Middle Eastern localities is given below), Persia, Algeria and Borneo : Lower Cretaceous, various levels. It has also been seen in material from the Upper Aptian, Mededine area, S. Tunisia. Reiss (1961) recorded it from the Aptian of Galilee, Israel, and regarded it as a dasycladacean alga. Dr. M. S. Edgell (*in litt.*, May 1960) also stressed the dasycladacean nature of Iranian material.

Most of these records clearly refer to the same organism. Comparison of Radoičić's and Elliott's descriptions show that the same features are common to both, though the type-figures selected emphasize slightly different characteristics. The organism occurs as hollow cylindrical or near-cylindrical tubes, circular in cross-section, and of varying external diameters up to 0·57 mm. The internal diameter varies from 54–70% of the external : lower values up to 60% or a little more are more common. The walls show a thin inner dark amorphous layer, finely micro-crystalline under a high power, and a thick outer layer (0·013 mm. and 0·104 mm. respectively in one typical example). This latter, which occupies most of the wall-thickness, is yellowish in thin-section appearance : it shows innumerable fine radial subparallel lines or cracks, and, at intervals, coarse canals which extend to widen at the outer surface to occasion shallow pores. In specimens of regular form these are

arranged at regularly-spaced levels, the pores alternating in position from level to level, and Radoičić, who figured them as dasyclad verticils of lateral branches, indicated (*op. cit.*, fig. 1) that the distance between adjacent external pores of one verticil was twice the distance between successive verticils. In Radoičić's type-figures, e.g. pl. 4, fig. 1, this regularity is very clearly shown, and other writers, e.g. Reiss 1961 (figs. 101, 105, etc.) also show this. In the types of *Hensonella* (Elliott 1960, pl. 8, fig. 1) this regularity is absent, and I drew attention to the irregularity. Reiss (*op. cit.* : 229), commenting on this, adds that the pores " occur in all suitably sectioned specimens ", meaning presumably sections taken at pore-level, and such specimens have been seen not uncommonly in slides of Middle East *Hensonella*.

The thick yellowish layer was described for *Hensonella* (Elliott 1960 p. 229) as aragonite. This was incorrect : it is calcite, and both Dr. A. Lees (Reading University) and Mr. J. McGinty (Iraq Petroleum) consider it derived from an original organic calcite structure.

Crushed examples from Algeria show the thick layer broken along radial partings, but in most cases still held together by the inner thin dark layer. If the crushing occurred during compaction, this suggests original organic nature for the thin layer, with some flexibility. Edgell (*in lit.*, 1960), who also supported the dasyclad nature of the organism, suggested that this layer may be the original algal wall, or thickened organic outer layer of the stem-cell, and this appears to be the view of Radoičić also (*op. cit.* : 38). That it was an original part of the organism is indicated both by its almost invariable presence irrespective of all but the very worst preservation, and by occasional specimens in which it is lined by a secondary inner layer of post-mortem calcite, possibly pre-burial, the actual tube-core within this being clear, transparent calcite deposited after burial from solution. The large canals which expend to the exterior are sometimes seen in random cut to reach this dark inner layer, and, following Reiss's reasoning on their external appearance, may similarly be supposed normally to do so when the sections are suitably orientated.

Summarizing, *S. dinarica* Radoičić and *Hensonella* Elliott were described from examples of the same organism, and the great majority of subsequent records refer to this same species. Slight differences in the two author's descriptions can be reconciled by examination of large sets of specimens. Since the fossil agrees in size, shape, and morphological structure with other dasyclads, and also occurs in suitable facies at suitable levels for this, Radoičić described it as a dasyclad, referring it to *Salpingoporella* and comparing it carefully with *S. mühlbergii* of the same age. A similar comparison is possible with the new *S. arabica*. This dasyclad reference seems to be the majority view of other workers, as expressed in synonymy or by comment.

In spite of this, there remain certain doubtful features which seem incompatible with a dasyclad origin. In living dasyclads, the deposition of the original aragonitic calcium carbonate is connected with the " assimilatory processes in the chlorophyll corpuscles " (Church 1895), and the calcified layers or structures built up of fine granules are amorphous. By contrast, the calcium carbonate of marine invertebrates (molluscs, brachiopods, corals, echinoderms, etc.) is deposited out of solution

by a wet membrane to give normally a lamellar structure, whatever the varied microstructure (fibrous, prismatic, etc.). This difference in structure makes the algal calcium carbonate much less resistant to diagenetic changes than that of almost any other fossil, with frequent disastrous results familiar to the palaeontologist.

Ignoring near-pure limestones in which the results of calcium carbonate solution-replacement mechanisms are common, it is seen that in the marly facies in which *Hensonella* (or *S. dinarica*) abounds the undoubted dasyclads such as *Actinoporella, Munieria* and *Cylindroporella* and other species of *Salpingoporella*, show skeletal remains preserved as white replacement calcite, coarsely crystalline in thin-section under moderate magnification. This is interpreted as diagenetic replacement of original aragonite. *Hensonella* stands out conspicuously by its translucent yellow radially-fibrous structure. This structure represents a diagenetic alteration of original calcite, not originally amorphous as in some other algae, and not of aragonite. The radial structure is original, a point emphasized by compaction-fractured specimens, and alteration has taken place in the wall-material between these partings, and not to obliterate them. Only very rarely and incompletely has a later change affected this resistant structure, and then not to the extent seen in associated dasyclads. These undoubted dasyclads, sealed in the same matrix and subjected to the same treatment, have behaved differently.

The thin inner dark layer is also anomalous for a dasyclad. If, as suggested by Edgell, it represents the thickened cell-wall of the stem-cell, then this is unusual in living dasyclads and not seen in fossil forms. In *Hensonella* it is consistently present under varied conditions of preservation from very different localities, which suggests that it originates from an original feature of the organism, even if diagenetically altered, and not from diagenesis itself. Moreover, although localized thickening of the outer stem-cell wall is known in the living *Dasycladus*, there is no trace of this preserved in the fossil *Pagodaporella* now considered related (see above, under *Pagodaporella*), even though the former presence of the structure is inferred.

In conclusion, I consider that this organism is best classified as a problematicum. The original comparison with a scaphopod appears unlikely, but the wall-material is not that of known dasyclads, and certainly not that of the associated dasyclads in the same beds.

Appendix. List of Middle East materials referred to *Hensonella*.

In Iraq, Qamchuqa Formation (Barremian level) of Sarmord, and Sarmord Formation (Barremian-Aptian level) of Sekhaniyan, both Sulemania Liwa ; subsurface Garagu Formation (Valanginian-Hauterivian) of Kirkuk no. 116 well Bottom lower Cretaceous, probably Valanginian, at Haushi, South Oman, Arabia. Common at Barremian-Aptian level in south-west Persia, and recorded from the Aptian of Galilee, Israel (Reiss 1961).

Genus ***TERQUEMELLA*** Munier-Chalmas 1877

1877 *Terquemella* Munier-Chalmas : 817.
1920 *Terquemella bellovacina* Munier-Chalmas ; Costantin : 1031–32.
1922 *Terquemella* Munier-Chalmas ; Morellet : 18.

DIAGNOSIS. Small, disc-like, lenticular or spherical calcareous bodies, with numerous tiny subdermal spherical sporangial cavities, the bodies themselves considered dissociated sporangial structures from Dactyloporeae (Dasycladaceae).

Terquemella bellovacina Munier-Chalmas

(Pl. 23, figs. 6, 7)

1920 *Trequemella bellovacina* Munier-Chalmas ; Costantin : 1031–32, figs. 13, 14.
1922 *Terquemella bellovacensis* Munier-Chalmas ; Morellet : 18, pl. 1, figs. 67–76.
1955b *Acicularis* sp. Elliott : 126, pl. 1, figs. 11 (right-hand fig.), 12.
1956 *Terquemella bellovacina* Munier-Chalmas ; Elliott : 332.

DESCRIPTION. Flattened, discoidal, solid calcareous bodies, approximately circular or well-rounded irregular in outline, diameter about 0·57 mm. (up to 0·65 mm. maximum seen), thickness 0·117 mm. (up to 0·143 mm. maximum seen). Hollow globular cavities of about 0·045–0·055 mm. diameter occur just within the outer edge of both surfaces, so that transverse (vertical) sections show two rows each of 8 cavities, and tangential-horizontal sections show cavities scattered over the whole section.

HORIZON. Palaeocene of France and of Iraq ; possibly also Central America (Johnson & Kaska 1965).

MATERIAL. Thin-sections from the Sinjar Formation (Palaeocene–Lower Eocene) of Sirwan (Sulemania Liwa), and Banik (Mosul Liwa), Iraq.

REMARKS. The Iraqi species is compatible with the details of the Morellets' description and figures, and the Munier-Chalmas' figures as reproduced by Costantin. *T. lenticularis* Pia, Rao & Rao (1937) from the Indian Eocene is similar but smaller.

Terquemella globularis Elliott

(Pl. 23, figs. 5, 8)

1956 *Terquemella globularis* Elliott : 332, pl. 2, fig. 2.

DESCRIPTION. Near-spherical or flattened ovoid solid calcareous body about 0·390 mm. in diameter, globular sporangial cavities 0·033–0·039 mm. in diameter just within outer edge over whole surface, so that equatorial sections show a circle of about eighteen of them, and tangential sections about 0·170 mm. in diameter show eight.

HORIZON. Palaeocene of Iraq.

MATERIAL. Iraq : Kolosh Formation (Palaeocene and Lower Eocene) of Bekhme and of Rowanduz, both Erbil Liwa ; Sinjar Formation (Palaeocene-Lower Eocene) of Sirwan, Sulemania Liwa, and of Chalki, Mosul Liwa.

REMARKS. Not known from outside Iraqi Kurdistan, though Praturlon (1966) records a *T.* cf. *globularis* from the same level in Italy. *T. parisiensis* Munier-Chalmas, from the Paris Basin Middle Eocene, is of similar shape but larger (diameter 0·5 mm.) and with fewer sporangial cavities.

"*TERQUEMELLA* s.l." sp.

Minute circular cross-sections of marginally sporangial bodies have been noted not uncommonly in Upper Jurassic and Lower and Upper Cretaceous rocks. These are presumably algal remains corresponding morphologically to *Terquemella*, but are unlikely to originate from Dactyloporeae like the Tertiary *Terquemella* spp. They show insufficient detail to be of much stratigraphic value. Similar bodies have been described elsewhere e.g. from the French Jurassic (Dangeard 1931).

Genus *TEUTLOPORELLA* Pia 1912

Teutloporella is mostly a Triassic genus, but Upper Jurassic species have been described from Switzerland (*T. obsoleta* Carozzi 1954) and Italy (*T. socialis* Praturlon 1963b). At Jebel Buwaida, Oman, masses of derived older rocks occur in the Upper Cretaceous Hawasina-complex. This rubble has yielded various Upper Jurassic algae, including fragmentary *Teutloporella* sp. This derived material is probably from an Oman occurrence *in situ* of one of these species, but is insufficient for description.

Genus *THAUMATOPORELLA* Pia 1927

Thaumatoporella was erected by Pia (1927) as a dasyclad genus for the Upper Cretaceous alga described as *Gyroporella parvovesiculifera* (Raineri 1922). Sartoni & Crescenti (1959) have shown that *Thaumatoporella* itself, although the name is valid, is not a dasyclad, and that it is the same as *Polygonella* (Elliott 1957) and *Lithoporella elliotti* (Emberger 1958b). It is a single-layer lamellar or encrusting alga of uncertain affinities, and only occasional specimens resemble a dasyclad in section. Remarkable for its long range (Rhaetic to Senonian), it is common at many levels in the circum-Mediterranean and Middle East, but its description has no place here.

Genus *THYRSOPORELLA* Gümbel 1872

DIAGNOSIS. Calcified tubular dasyclad showing successive verticils of radial branches, each branch showing several repeated divisions into smaller branches and branchlets, all but the last divisions swollen.

Thyrsoporella silvestrii Pfender

(Pl. 23, figs. 1–4 ; Pl. 24, fig. 5)

1940 *Thyrsoporella silvestrii* Pfender : 227.
1955b *Thyrsoporella silvestrii* Pfender ; Elliott : 129, pl. 1, fig. 10.
1960 *Thyrsoporella silvestrii* Pfender ; Elliott : 225, 226.
1966 *Thyrsoporella silvestrii* Pfender ; Massieux : 113, pl. 1, figs. 1–8. (Part 2 of this study (see Bibliography), in which Mlle. Massieux refers *T. silvestrii* to *Belzungia*, was seen too late for proper discussion in this work. However, the specimens now studied from the Middle East show the solid walls of *Belzungia*, but the branch-system appears like that of *Thyrsoporella*).

DESCRIPTION. Thick-walled, tubular, cylindrical calcareous dasyclad, length

(observed) up to 3·5 mm., external diameter up to 0·78 mm., internal diameter from 33–50%, figures in the lower half of this range being most common ; verticils of horizontal branches close-set, about 9 per mm. of tube-length, with six or more branches per verticil. Each primary branch is considerably wider than high, and in transverse section is markedly swollen with curved sides : a thin vertical partition marks the beginning of division into two secondaries, smaller but similarly swollen, and these in turn each divide into four little swollen tertiaries. These each divide into several terminal branchlets, probably four, which reach the outer surface as pores. On a specimen of 0·754 mm. external diameter the maximum branch-diameters in transverse section were primary, 0·156 mm. ; secondary 0·117 mm., tertiary 0·039 mm., and quaternary, about 0·015 mm.

Horizon. Uncommon in Palaeocene–Lower Eocene of Middle East, but common in the Middle Eocene of the same area. Listed by Pfender (1940) from the Eocene of Madagascar.

Material. In Iraq, seen from the Palaeocene–Lower Eocene Kolosh Formation of Sedelan, Sulemania Liwa, and from the Palaeocene of the Ghurra scarp, west-southwest of Wagsa, Diwaniyah Liwa. In Arabia, from the Palaeocene–Lower Eocene of Sahil Maleh, Batinah Coast, Oman, and from the Palaeocene of Aqabar Khmer, Hajer, Hadhramaut. See also Hadhramaut record of Beydoun (1960 : 146). (The much more abundant Middle Eocene occurrences are discussed below : one of Pfender's records, however, is from the Palaeocene of Turkey.)

Remarks. *Thyrsoporella silvestrii* Pfender was described from Egyptian Middle Eocene material and compared with the European *Thyrsoporella cancellata* Gümbel from the French Middle Eocene. This latter (L. & J. Morellet 1913) is a longer, thinner, more fragile species, with a proportionally wider stem-cell (66% of external diameter). Pfender recorded her species from the Middle Eocene of Egypt and Somalia, and also from Syria, Turkey and Madagascar. In the collections now studied it has been seen commonly in the Middle Eocene of north and south Iraq, and of Oman.

In the Palaeocene–Lower Eocene occurrences studied for this work the species is rare. The records are all based on random sections, and it is possible that with a good series of specimens these older records might prove to be of a species or variety distinguishable from Pfender's species : this has not been possible so far. Pfender (1940) did not illustrate her paper, though this was remedied by Massieux (1966), and the Morellets worked on dissections of solid specimens from the French Eocene. The opportunity is now taken to illustrate *Thyrsoporella silvestrii* by figuring some good thin-sections of Arabian (Oman) material from the Middle Eocene.

Genus ***TRINOCLADUS*** Raineri 1922

Diagnosis. Calcified tubular dasyclad showing successive verticils of radial branches, each branch showing outwardly-widening primaries giving rise to several similar-shaped secondaries, and these in turn to bunches of tertiaries : branches of the lower verticils may not show the full detail. Branches not alternate in position from verticil to verticil.

Trinocladus tripolitanus Raineri

(Pl. 24, figs. 3, 4)

1922 *Trinocladus tripolitanus* Raineri : 79, pl. 3, f. 15, 16.
1936 *Trinocladus tripolitanus* Raineri ; Pia : 5, pl. 2, text-fig. 3.
1960 *Trinocladus tripolitanus* Raineri ; Elliott : 224.
1966 *Trinocladus tripolitanus* Raineri ; Massieux : 114, pl. 2, fig. 1.

Description (based on Pia). Tubular cylindrical dasyclad, probably slightly club-shaped, length (observed) up to 3·36 mm., external diameters (different parts of thallus) from 0·47–0·68 mm., corresponding internal diameters 0·16–0·19 mm. (34–28%). Successive verticils, 9 or 10 per mm. of tube-length, are each of about 8 horizontally-directed branches, which usually are not alternate in position in successive whorls. Each primary branch is club- or paddle-shaped in transverse section, widening rapidly from a narrow junction with the stem-cell and extending outwards through about half the wall-thickness : it then gives rise in turn to several smaller but similarly-shaped secondaries (perhaps five or six), and each of these in turn to a cluster of about six slim short tertiaries reaching the exterior as pores. Branches from lower verticils do not show tertiaries and may have been sterile.

Horizon. Cenomanian or Turonian of Libya, North Africa (Raineri 1922 ; Pia 1936) : Turonian of France (Pfender 1940) and of Iraq and Trucial Coast, Arabia : Upper Cretaceous of Czechoslovakia (Andrusov 1939).

Material. Subsurface Turonian of Ras Sadr no. 1 well, Abu Dhabi, Trucial Oman, Arabia, and of Musaiyib no. 1 well, Hilla Liwa, Iraq.

Remarks. The Middle East occurrences of this species are known only by random thin-sections, which however correspond well in dimensions and detail to those of the Libyan type-material ; external diameters observed are 0·650–0·702 mm., with corresponding internal diameters of 0·182–0·208 mm. (28–30%). Moreover, other algae associated at the type-locality are also seen in the Middle East occurrences : *Dissocladella undulata* (Raineri) Pia at both localities and the codiacid *Boueina pygmaea* Pia as well at Ras Sadr.

Trinocladus perplexus Elliott

(Pl. 24, figs. 1, 2, 6, 7)

1955b *Trinocladus perplexus* Elliott : 128, pl. 1, figs. 16–18.
1960 *Trinocladus perplexus* Elliott ; Elliott : 225.

Description. Tubular cylindrical calcified dasyclad, probably originally slender club-shaped. Length (incomplete) up to 2·5 mm. seen, with external diameters increasing from about 0·32 to 0·44 mm., and the proportion of internal diameter to external constant at 53%. Fragments of smaller examples of 0·26 mm. diameter show an internal diameter of only 40%. The wall shows consecutive horizontal verticils of lateral branches : in the large example quoted the verticils are spaced at about 17–19 per mm. in the lower, slimmer portion of the tube, diminishing to about 12 per mm. later. Each verticil consists of 7–10 branches : these communicate with the stem-cell cavity by rounded-rectangular pores. Each short thick primary

divides into four secondaries : in the older, slimmer parts of the thallus this is all the branching seen, but in the later, wider portions each secondary divides into four tertiaries which reach the exterior as pores.

HORIZON. Palaeocene–Lower Eocene of Iraqi Kurdistan.

MATERIAL. From the Kolosh Formation (Palaeocene–Lower Eocene) of Surdash, Sulemania Liwa ; Koi Sanjak, Erbil Liwa, and Sundur, Mosul Liwa : all in northern Iraq.

REMARKS. *Trinocladus perplexus* is the almost invariable companion of the codiacid *Ovulites morelleti* Elliott in the clastic facies or Kolosh green-rock sands of Kurdistan, where occurrences of the two species far outnumber occasional records of other algae. *Trinocladus* is however missing from the varied, richly algal Sinjar limestone and marl facies of the same age-range, where *O. morelleti* is also abundant. This ecological distribution is considered elsewhere in this work.

T. perplexus has not been seen outside this limited area ; its distribution is thus very different from that of the related *Thyrsoporella silvestrii*, or indeed from the older species *Trinocladus tripolitanus*.

Trinocladus radoicicae sp. nov.

(Pl. 24, fig. 8)

DESCRIPTION. Tubular cylindrical calcified dasyclad, probably originally slender club-shaped. Length unknown, fragments up to 1·0 mm. seen ; maximum observed diameter 0·75 mm. d/D ratio about 33%. Smaller transverse sections of 0·42 mm. and 0·34 mm. diameters show a verticil of seven branches : the primaries swell out markedly before dividing into thinner secondaries (probably four) and these in turn into several tertiaries. Specimens of smaller diameter show only primaries and secondaries.

HORIZON. Maestrichtian of Iraqi Kurdistan and (subsurface) Dukhan, Arabia.

SYNTYPES. The specimens figured in Pl. 24, fig. 8 from the Tanjero Clastic Formation (Maestrichtian) of Diza, Erbil Liwa, Iraq. V. 52116.

OTHER MATERIAL. Several random thin-sections from the same formation and horizon, Diza, Erbil Liwa, and Balambo, Sulemania Liwa, Iraq. Also similarly from the subsurface top Aruma of Dukhan no. 1 well, Qatar, Arabia.

REMARKS. Although the green-rock clastic facies continues in Iraqi Kurdistan from Tanjero Formation (Maestrichtian) to Kolosh Formation (Palaeocene), it contains different species of the codiacid *Ovulites*, *O. delicatula* Elliott and *O. morelleti* Elliott respectively. These are presumably successional in evolution. As already remarked, *Trinocladus perplexus* is the constant companion of *O. morelleti* in the Palaeocene ; *T. radoicicae* is now described as the Maestrichtian associate of *O. delicatula*. It is, however, rare and fragmentary when compared with *O. delicatula* (itself much less common than *O. morelleti*).

T. radoicicae is similar in form, approximate size and succession of branch-complexity within the one thallus to *T. perplexa*. It differs noticeably in the form

of the branches : those of *T. perplexa* are spindly compared to the very swollen primaries of *T. radoicicae*, where each branch takes proportionally more space and hence there are fewer branches per verticil.

This species is dedicated to Mme. R. Radoičić of Belgrade, Jugoslavia, as a tribute to her many contributions to palaeophycology, and friendly correspondence with me.

Genus ***TRIPLOPORELLA*** Steinmann 1880

DIAGNOSIS. Club-shaped calcified dasyclads with large stem-cell, close-set verticils of numerous branches each consisting of an elongate cylindrical primary containing sporangial bodies, and dividing into several thin hair-like secondaries.

REMARKS. The large and showy *Triploporella* spp. of the Upper Jurassic and Cretaceous are curiously ill-represented in the Middle East material now studied. No further material of *Triploporella fraasi* (Steinmann 1880 ; 1899) from the Lebanese Albian has been examined : most of this author's descriptive detail came from his Mexican specimens and not from the ill-preserved Lebanese fossils. Three other Middle East records of the genus known to the writer are all Cretaceous, all represented by very few random thin-sections, and none specifically determinable. Two, from the Lower Cretaceous of Burum, Wady Hiru Basin, Hadhramaut, and from the subsurface Garagu Formation (Valanginian-Hauterivian) of Makhul no. 1 well, Mosul Liwa, Iraq, are compatible in size with such a species as *T. marsicana* Praturlon from the Italian Barremian-Aptian. The third, from the Qamchuqa Formation (Aptian-Albian level) of Sarmord, Sulemania Liwa, Iraq, is much smaller than any described species.

IV. THE STRATIGRAPHIC SUCCESSION OF DASYCLAD ALGAE

The stratigraphic ranges in the Middle East of most of the dasycladaceae described in this work are set out in Fig. 6. Before discussing these in relation to the different geological levels involved, the general reliability of the family for stratigraphic purposes must be considered.

Dasycladaceae are sessile benthos with well-defined coastal ecologic requirements, the latter discussed below (p. 92). It is, therefore, rare for them to show the limited substage range of an ammonite species, and they are inevitably influenced by facies. Against this, the Tethyan coasts and shelf-seas furnished a long succession of suitable habitats for growth and entombment, and dasyclad euryhalinity permitted frequent proliferation in emergent areas when their abundance as microfossils matched that usual with marine foraminifera, themselves scarce or banal under these conditions. In the favoured area of the Middle East, therefore, (and this probably applies to many other areas in the Tethyan belt), I have often found it possible to date to stage-level by a consideration of dasyclads in association with other algae, and their relative abundance (cf. Elliott, 1960). Supplementary confirmation from other fossils has been welcome, but rarely contradictory.

A similar conclusion was independently reached by Praturlon (1966), for the Liassic to Palaeocene algae of the central Apennines, Italy. It is of interest to compare the

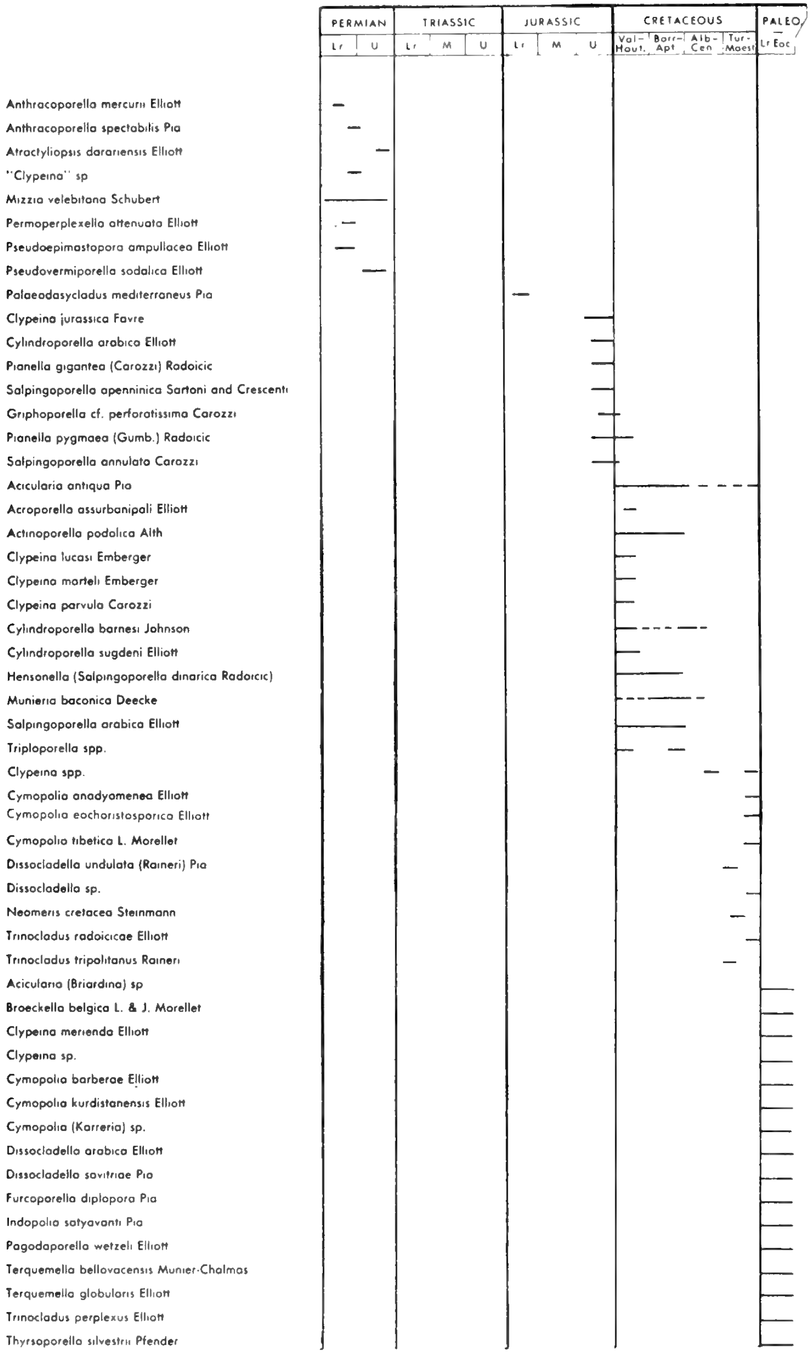


FIG. 6. Stratigraphic ranges of dasyclad algae in the Middle East.

ranges of 29 dasyclads listed by him with the 45 now shown for the same time-interval in fig. 6. A general correspondence of restricted ranges, with individual, local differences, may be observed.

Permian

The dasycladaceae recognized from the Iraqi Permian and their distribution therein are shown in Fig. 7. This Permian succession is approximately 800 m. thick, and was sampled by Wetzel and others through complete successions near the localities of Ora and Harur, in the north of Mosul Liwa, near the Turkish frontier. The general succession is set out in Dunnington, Wetzel and Morton (1959) where the whole series of thick upper and lower limestone divisions, separated by a thinner evaporitic development, is named the Chia Zairi Formation ; Hudson (1958) has named the two thick limestone divisions, so that the succession, from bottom to top, comprises Zinnar Formation, Satina Evaporite Formation and Darari Formation.

The Zinnar rests unconformably on Carboniferous (Tournaisian). The Darari, at its top, shows evidence of progressive shallowing, though the actual contact with the overlying Triassic is said to be abrupt.

Of the rich faunas collected, only two, both from the Zinnar, have been adequately investigated. A coral fauna, from the *Wentzelella* limestones at about the middle of the Zinnar, was compared by Hudson (1958) with similar faunas elsewhere in Asia, the latter often including *Neoschwagerina*, especially *N. cratulifera* (Schwager) " which could quite well be the age of the *Wentzelella*-Limestones of Iraq ". This would be Artinskian-Kungurian (or Leonard-Word). A fusulinid-fauna occurs near the base of the Zinnar : this was studied by Lloyd (1963) who thought it " somewhat older " than a comparable Iranian assemblage dated as of *Parafusulina*-zone age i.e. a possible Sakhmarian-Artinskian (Wolfcamp-Leonard) age for this lower part.

No other detailed faunal evidence for age is at present available above these levels, though the upper Darari is similar to the north Italian *Bellerophon*-limestone described by Accordi (1956). It may be that sedimentation was more or less continuous throughout, up to the Triassic contact, and that the Zinnar-Satina-Darari correspond to ?Sakhmarian (part), Artinskian-Kungurian-Tartarian, but this remains to be proved by detailed analysis of the faunas. It is unlikely that the boundaries of the Satina will correspond with stage levels. Against this lack of detail the ranges of the dasyclads are of some interest.

Mizzia velebitana ranges from near the base of the Iraqi Permian to near the top, accompanied by the nondasyclads *Gymnocodium bellerophontis* and some *Permocalculus* spp. The other dasyclads have very different ranges. *Anthracoporella mercurii* is confined to the basal beds of the Zinnar : *Pseudoepimastopora ampullacea* occurs in the Zinnar only, as do the non-dasyclad *Ungdarella* Maslov and the new *Permoperplexella*. *Atractyliopsis darariensis* occurs only near the top of the Darari, and *Pseudovermiporella sodalica* only within this formation. " *Clypeina* sp. " marks the emergent conditions of the Zinnar-Satina contact level.

It is probable that a fresh sampling, carried out primarily for the collection of

algae, would add much to our knowledge of these fine sections and of the Permian in general, and possibly permit an algal zonation, from dasycladaceae and other families, of potentially wide application in Asia.

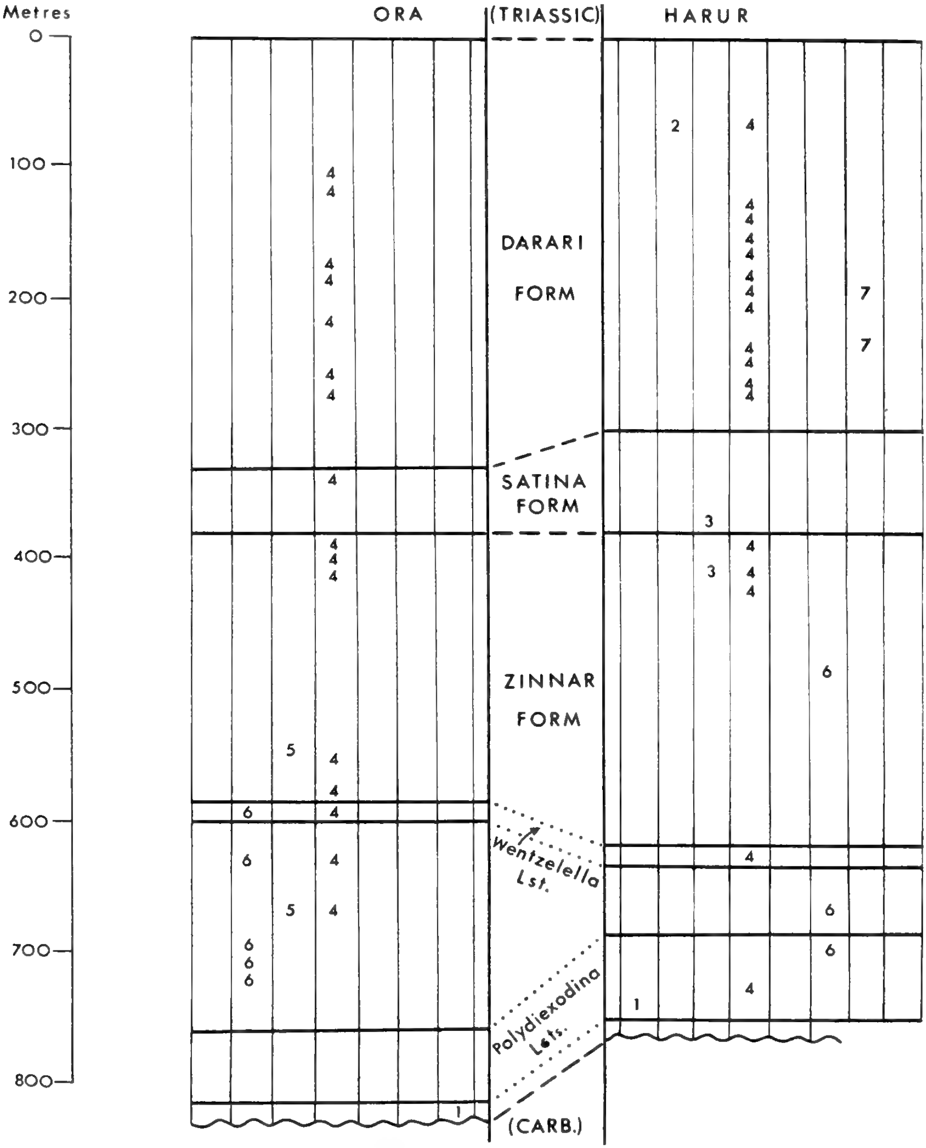


FIG. 7. The Permian dasyclads of Iraqi Kurdistan at Ora and Harur, Mosul Liwa. 1. *Anthracoporella mercurii* Elliott. 2. *Atractyliopsis darariensis* Elliott. 3. "*Clypeina*" sp. 4. *Mizzia velebitana* Schubert. 5. *Permoperplexella attenuata* Elliott. 6. *Pseudoepimastopora ampullacea* Elliott. 7. *Pseudovermiporella sodalica* Elliott.

Lower Jurassic

The occurrence of the Liassic *Palaeodasycladus* in the Lower Musandam of Oman is compatible with the age from other evidence (Hudson & Chatton 1959), but as the alga is so far recorded only from one level it shows no more than as an easterly occurrence of this well-known Mediterranean fossil.

Upper Jurassic–Lower Cretaceous

The ranges of various dasyclads in the Middle East at these levels are shown on the chart. Reference to the European literature indicates different local ranges for some of these species. Thus *Actinoporella podolica* is Portlandian at the Galician type-locality, Portlandian–Valanginian in Switzerland, Portlandian-Hauterivian in Italy, and Valanginian-Aptian in the Middle East. This probably reflects facies-preference along successive Tethyan coasts, partly obscured by some occurrences being preserved in off-shore debris-facies. It is of course possible that a suite of similarly well-preserved specimens from each locality would permit successional subdivision of the species. The type-material comprises loose, dissociated verticils, whereas most of the other records are from random thin-section material. However, this must await future studies. In association with other microfossils, *A. podolica* is a useful species in the Middle East, as are most dasyclad remains. *Munieria baconica* shows a somewhat similar range, with varying local occurrences. By contrast, such species as *Clypeina lucasi* and *C. marteli* occur only at the same level in Oman as that of the Algerian types. The European ranges of a dasyclad species, and the details of its Middle East occurrences, will already have been noted under each species-description.

The algal dating of the Jurassic–Cretaceous contact in the wholly marine Tethyan succession is of some importance. Over large type-areas of western Europe a varying thickness of nonmarine Purbeck-facies strata occurs between undoubted marine Upper Jurassic and Lower Cretaceous. This Purbeckian is conventionally assigned to the Jurassic, though the studies of Donze (1958b) on the Jura area, and Casey (1963) on England, suggest that much of it is Cretaceous (see also Bartenstein, 1965). In southern France, where marine Tithonian is succeeded by marine Berriasian, the two may be distinguished by their ammonite faunas. In many other Tethyan limestone successions at this level the absence of ammonites, whether due to their non-occurrence in the fauna or their non-availability as in samples from bore-holes, necessitates estimation of the junction from microfossils in thin-section. The foraminifera give no clear picture, and tintinnids are confined to a special stratigraphical facies. Dasyclad algae are often abundant ; in my experience, if determined carefully, with a full knowledge of their recorded ranges elsewhere and used in conjunction with non-dasyclad algae such as *Permocalculus* spp. and various non-algal fossils such as the hydrozoan *Cladocoropsis*, it is usually possible to give an accurate age-determination.

Upper Cretaceous

The dasyclads of the Middle East Upper Cretaceous are fewer in number than those

of the Lower Cretaceous. The most important florules are the *Trinocladus tripolitanus* assemblage of about Turonian age, common to North Africa, Iraq, Trucial Oman and perhaps elsewhere, and the Maestrichtian assemblage of which *Cymopolia tibetica* also occurs in the Himalayas.

Palaeocene–Lower Eocene

The rich dasyclad flora of Kurdistan and elsewhere occurs throughout the Palaeocene and Lower Eocene. In Kurdistan it has been possible to date the two stages foraminiferally in certain sections e.g. at Kashti, also at Sinjar and Koi Sanjak (Van Bellen 1959) and unpublished reports. The algae show no consistent stratigraphical differentiation throughout, though there is a sharp change from the Cretaceous below and to the Middle Eocene above. This flora contains elements known from the Indian " Danian " of the Trichinopoly coast (recently correlated on foraminiferal and other evidence with the Lower Palaeocene elsewhere : Sastry & Rao 1964, Rajagopalan 1965) and from the European Montian, and it appears that algally at any rate the Palaeocene commences with the immediate post-Maestrichtian, which is also the opinion of some workers on foraminifera (e.g. Berggren 1964). In this connection it should however be noted that the Tethyan Danian-equivalent (if and when present) may not easily be recognizable by comparison with the northern European type-development.

V. THE GEOGRAPHICAL DISTRIBUTION OF TETHYAN ALGAE

The most casual student of Tethyan fossils is struck by the very wide east-west distribution of Tethyan facies and fossils, which occur in disconnected outcrops over enormous distances : there is often more difference between the south of England and the south of France at the same level than correspondingly between Spain and the Middle East, India or even Borneo. The algae are no exception to this : in the Permian *Mizzia velebitana* and the non-dasyclad *Gymnocodium bellerophontis* have a world-wide latitudinal distribution, and in the Cretaceous *Neomeris cretacea* occurs in both Mexico and the Middle East. The Liassic *Palaeodasycladus* ranges from Algeria to Iran, and the Upper Jurassic algal suite from France and Switzerland to the Persian Gulf, while *Terquemella* is found in the Palaeocene–Eocene of Central America, Europe, the Middle East and India. It is true that there are curious absences and near-absences from the collections studied, e.g. the Jugoslav Permian *Velebitella* (also known from Turkey, Güvenç 1965) and the Italian Cretaceous *Triploporella* spp., both of which one would expect to find conspicuously at the appropriate levels, but future collecting may well remedy this.

With this wide marginal-Tethyan distribution of the same or closely-related species it is difficult at most levels to detect evidence of directional migration. The Palaeocene–Lower Eocene of the Middle East, however, shows an apparent mingling of eastern and western elements. *Indopolia* and *Dissocladella* from the east are there, associated with *Cymopolia* from the west. These eastern and western forms quoted are otherwise mutually exclusive at this level to India-Pakistan and Europe,

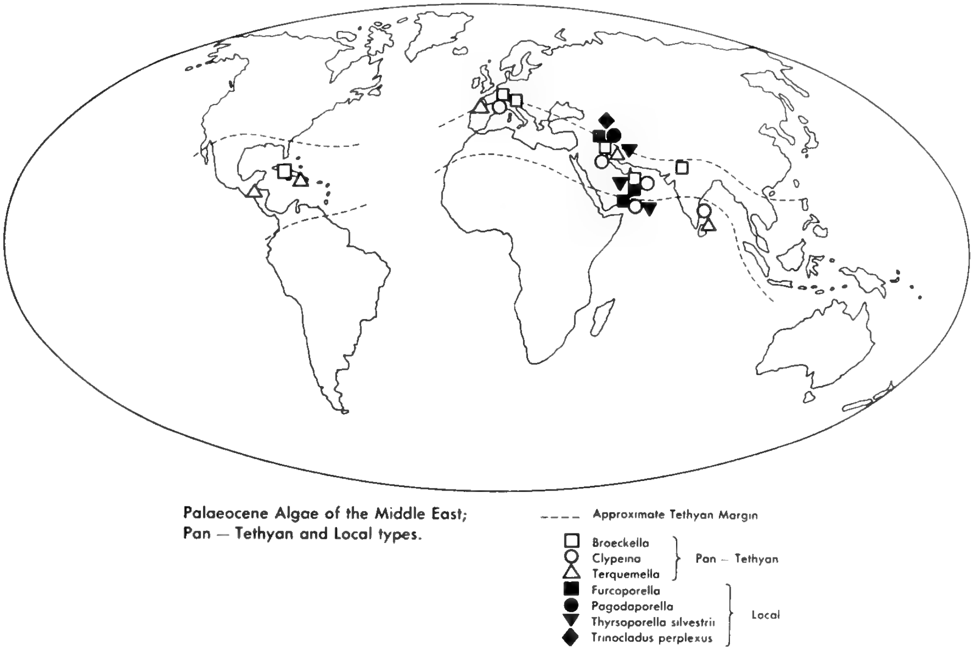

Palaeocene Algae of the Middle East;
Pan — Tethyan and Local types.
Approximate Tethyan Margin
Broeckella
Clypeina
Terquemella
Pan — Tethyan
Furcoporella
Pagodaporella
Thyrsoporella silvestrii
Trinocladus perplexus
Local

FIG. 8.

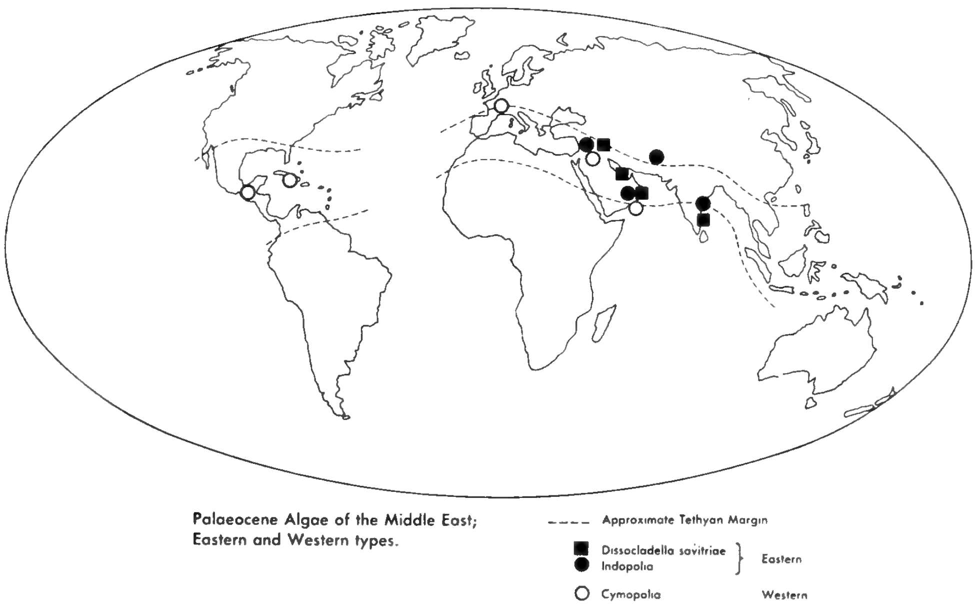

Palaeocene Algae of the Middle East;
Eastern and Western types.
Approximate Tethyan Margin
Dissocladella savitriae
Indopolia
Eastern
Cymopolia
Western

FIG. 9.

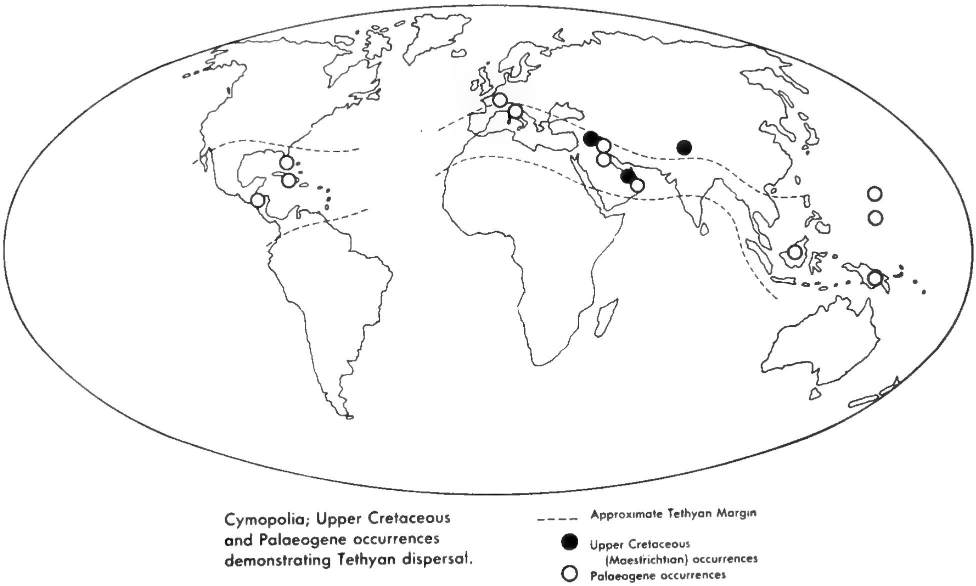

Cymopolia; Upper Cretaceous and Palaeogene occurrences demonstrating Tethyan dispersal.
Approximate Tethyan Margin
Upper Cretaceous (Maestrichtian) occurrences
Palaeogene occurrences

FIG. 10.

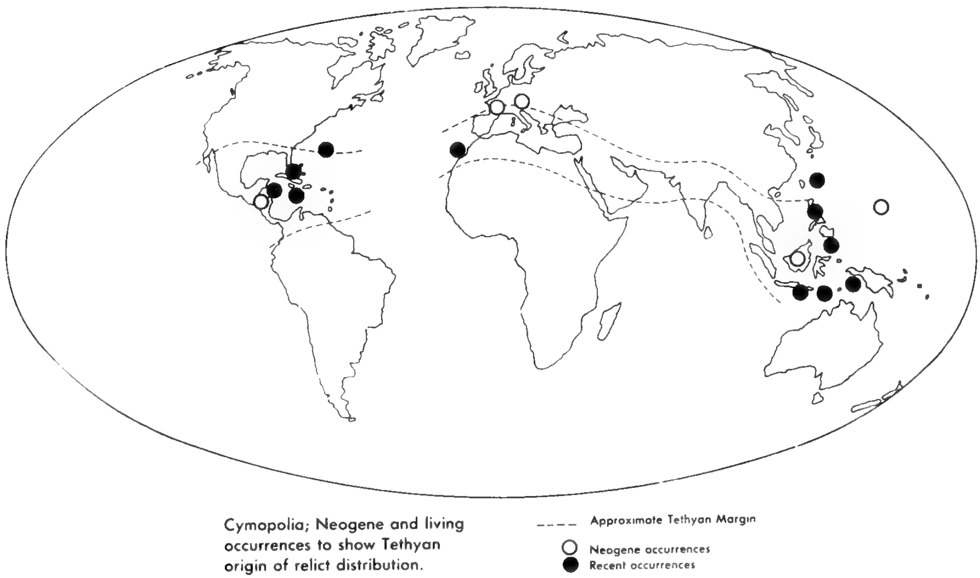

Cymopolia; Neogene and living occurrences to show Tethyan origin of relict distribution.
Approximate Tethyan Margin
Neogene occurrences
Recent occurrences

FIG. 11.

Trinocladus, an extinct dasyclad; distribution showing relict — occurrence in the Palaeocene.

---- Approximate Tethyan Margin

▽ Trinocladus Spp (Upper Cretaceous)

▼ Trinocladus perplexus (Palaeocene — Lr. Eocene)

FIG. 12.

Thyrsoporella, an extinct dasyclad; distribution showing post-Palaeocene dispersal.

---- Approximate Tethyan Margin

▲ Thyrsoporella (Palaeocene — Lr. Eocene)

△ Thyrsoporella (M. Eocene)

FIG. 13.

but *Broeckella*, *Clypeina* and *Terquemella* occur in both as well as in the Middle East, and *Pagodaporella* is so far known only from the Middle East. This assortment of genera in the very sector of the Tethys which in mid-Tertiary was to become the land barrier dividing the marine Mediterranean-Antilles from the Indo-Pacific is no doubt significant for the modern discontinuous distribution of dasyclads, even if most of the genera quoted are now extinct. The distribution-maps (Figs. 8–14) illustrate different aspects of past and present dasyclad occurrences. The value of these dated fossil occurrences may be seen by a comparison with the distribution-maps of Svedelius (1924) which, whilst taking account of former continuous sea-ways, show only Recent distribution.

The work of Kaever (1965), on the micropalaeontology of Afghanistan, contains numerous records of Tethyan algal species familiar in the Middle East. Unfortunately this paper came too late to my notice for inclusion of the detailed species records.

VI. ECOLOGY

At the present day dasyclads are a relatively inconspicuous element in marine algal floras. Although life has sometimes taken me to warm-water shores, I have never seen or collected living dasyclads. Their ecology has been briefly summarized by Pia (1920), Cloud (1962) and Johnson (1961b), all palaeontologists, for comparison with fossil occurrences. They occur in warm shallow coastal waters in sheltered situations in tropical and subtropical seas, and in areas marginal to the latter, such as the Mediterranean. Their maximum abundance is said to be from low-tide level to 5–6 m. depth, extending down in diminishing abundance to 10 m., and with scattered occurrences below this to 30 m. or more, depending on intensity of illumination and

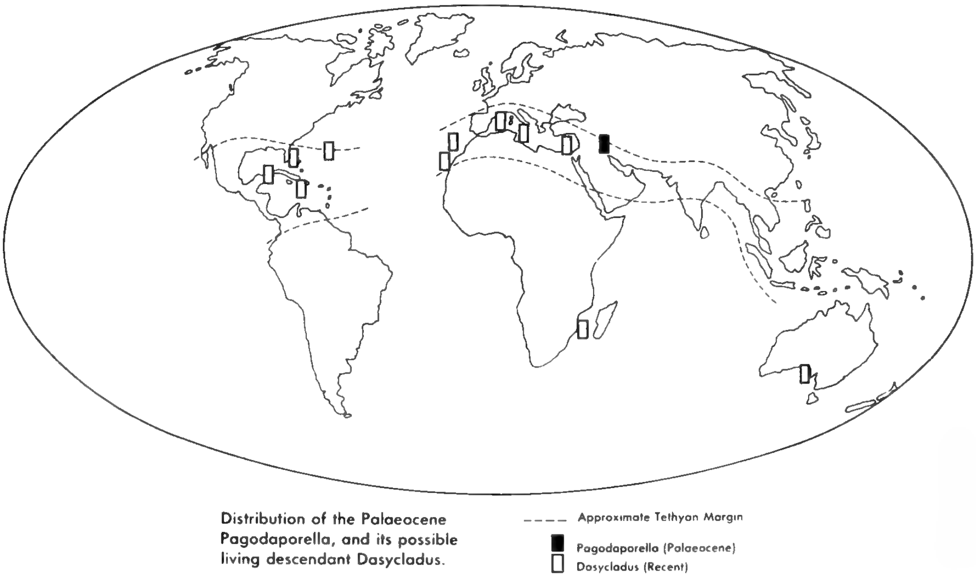


FIG. 14.

clearness of water. However Edelstein (1964) records *Dasycladus vermicularis* (Scop.) Krasser in the eastern Mediterranean from 18–90 m., represented by well-grown individuals larger than those in the littoral flora ; it seems clear that inferences as to exact water-depths should not be drawn from fossil dasyclads alone. The sheltered parts of coastal bays and some lagoons are favoured habitats, and they are tolerant of the reduced salinities which may occur there. Probably, like most non-stenohaline marine organisms, they are euryhaline and have a limited tolerance for temporary conditions of increased salinity. Such general conditions are associated geologically with regions of uplift, and the fossil dasyclad record confirms this. As with most marine organisms they have a scattered distribution outside the optimum habitat, and Chapman (1961 : 104, 106) gives records of *Neomeris* on mangrove roots and a stunted population of *Batophora* in an exposed situation.

Konishi & Epis (1962) gave a distribution-map showing clearly the restriction of living *Neomeris* spp. to areas within the marine isocrymes for 20 °C, and a table giving bathymetric occurrences. They discussed the implications of this evidence for the fossil occurrences, concluding that the fossil species probably occupied similar warm-water environments, then more widely-spread, as is generally accepted (e.g. Davis & Elliott 1957 : 269).

So far as can be deduced from associated fossils and the nature of the rock, the extinct dasyclad floras of the Middle East (and elsewhere) favoured exactly similar environments in the past to those now favoured by their descendants. However, at times of maximum abundance, dissociated debris of calcareous dasyclad origin forms a conspicuous element in sediments deposited further out to sea, for which the term " debris-facies " was introduced (Elliott 1958a).

In the Permian succession of northern Iraq the dasyclad *Mizzia velebitana* is abundant at many horizons through most of a thickness of over 800 m. It is accompanied throughout by profuse remains of *Gymnocodium bellerophontis* and various species of *Permocalculus*. These Gymnocodiaceae have been variously interpreted (Pia 1937 ; Elliott 1955a ; Konishi 1961) as Codiaceae (Chlorophyceae) or Chaetangiaceae (Rhodophyceae) ; whatever the taxonomic position, both the families cited are quiet-water marine algae today as compared with the reef-forming melobesioids. It is significant that amongst all the Iraq Permian algae there occurs only one solenoporoid, a group supposedly ancestral to the melobesioids (Elliott 1965a) and similarly of reef and shoal facies, and that uncommonly ; *Solenopora centurionis* Pia. The *Mizzia-Gymnocodium* association, sporadically abundant in the lower or Zinnar Formation, disappears within the lowest beds of the median Satina Evaporite, along with other algae and almost all fossils, but reappears in the uppermost beds, and so into and through the Upper or Darari Formation. At the top this latter shows signs of transition to the overlying but unconformable Lower Triassic, which is in the Werfenian alpine facies without remains of algae.

The Iraqi Permian contains some beds with a predominantly coral, brachiopod or crinoid fauna (Hudson 1958 ; Dunnington, Wetzel & Morton 1959). Moreover, in some of the algal beds the coarse colander-pore *Mizzia*- segments are worn, indicating post-mortem drifting from the position of growth. But the algal beds are suffi-

ciently numerous to prove the continued growth of *Mizzia* and other dasyclads in coastal environments throughout the whole period of deposition, even though the sediments at the sampled successions of Harur and Ora reflect the intermittent shifting of this coastline. The minor dasyclad elements, *Anthracoporella, Atractyliopsis, Clypeina, Permoperplexella, Pseudoepimastopora* and *Pseudovermiporella* do not in any way conflict with the picture drawn from the dominant *Mizzia*. The very scarce *Clypeina* occurs at the top of the Zinnar and the bottom of the Satina Evaporite, a fact consonant with later opinions on the facies behaviour of the Mesozoic species.

Rezak (1959) dealing with the Saudi Arabian Permian, observed the occurrence-relationships and associations of *Epimastopora, Gymnocodium* and *Mizzia*, and suggested a possible algal depth zonation as explanation. In Iraq *Pseudoepimastopora* is confined to the lowest division, the Zinnar Formation, in which particularly well-marked coral and brachiopod beds occur and in which the *Gymnocodium-Mizzia* beds are more sporadic than in the later beds. From the sampling available to me, I cannot interpret my records along the lines of Rezak's suggestion, but such depth-zonation may well have existed.

The rarity of Triassic dasyclads in the Middle East has already been noted ; it forms a remarkable contrast to the diplopore-limestone of alpine Europe. The evidence of the Kurdistan Geli Khana and Kurra Chine formations (Middle and Upper Trias) suggests originally unfavourable conditions.

Two Jurassic algal occurrences give a clear picture of the original ecology. The *Palaeodasycladus*-bed in the Liassic portion of the Musandam Formation in peninsular Oman, Arabia, shows a limestone, now partially dolomitized, crowded with healthy, full-grown specimens of well-developed *P. mediterraneus*, whole and broken. Associated are concentric nodules of probable cyanophyte algal origin. The picture is of an extensive spread of the dasyclads in clear, shallow warm water, on a limy bottom: a typical habitat.

In the Upper Jurassic of Qatar and elsewhere in the Persian Gulf area the " Arab zone " (Kimmeridgian-Tithonian) yields a florule of *Clypeina jurassica, Salpingoporella annulata* and *Cylindroporella arabica* occurring in fine-grained and oolitic limestones : associated are numerous crustacean coproliths, *Favreina salevensis* (Paréjas), and small gastropods and foraminifera. The picture is again of shallow, clear limy-bottomed waters, possibly lagoonal or enclosed ; the snails and crustacean traces may be indirect evidence of an abundant growth of non-calcarous green algae of which nothing certain now remains. The modern eel-grass beds of the West Indies and Bahamas would be comparable : Chapman (1961 : 9) gave a Jamaican record of numerous Codiaceae and *Dasycladus* sp. from this environment.

In the same general area of southeastern Arabia a very different picture is given by the Lower Cretaceous algal beds penetrated in the Fahud no. 1 boring. Here the rock is formed of rounded pieces of the crusting problematic algae *Lithocodium* and *Pycnoporidium*, with similar-sized pieces of stromatoporoids and less frequent coral, and rare valves of cemented thecidean brachiopods. Associated are numerous examples of segments of the dasyclad *Cylindroporella sugdeni*. This is reef or shoal

debris, current-swept and well-rounded, and washed out some distance from the organic growths which furnished it, even if to no great depth. The *Cylindroporella*, a plant believed to be possibly somewhat similar in form to the living segmented *Cymopolia*, owes its preservation to the relatively large, stumpy, well-calcified segments surviving transport : the plants themselves would have grown on the lee side of the shoals.

In the Iraqi Cretaceous, from the base up to Albian level, dasyclad remains are not uncommon and sometimes abundant. The principal genera involved are *Actinoporella*, *Cylindroporella*, *Munieria* and *Salpingoporella* ; *Acicularia*, *Acroporella*, *Clypeina*, *Pianella* and *Triploporella* also occur. The commonest non-dasyclad alga is *Permocalculus* (see Elliott 1960 for full algal lists). Complete or near-complete fossils, whether tubes, segments or verticils, are relatively uncommon and usually occur in a fragmentary condition, in limy marls and argillaceous limestones. This, the " debris-facies ", has been described by me (Elliott 1958a), where I interpreted it as off-shore sedimentation in which fragments of littoral calcareous algae were sedimented out at sea with inorganic grains of smaller size and higher specific gravity. A comparison was made with modern sediments around Pacific atolls, where fragmentary *Halimeda* and large foraminifera, roughly comparable with the Cretaceous *Permocalculus* and *Orbitolina* respectively, are washed out to sea. No exact analogy proved possible : the very extensive Cretaceous deposits were formed on inter-orogenic shelf-seas then more widely developed than with today's post-glacial submarine topography, and the wealth of Cretaceous littoral green algae proliferated before the maximum, later development in the Tertiary and present-day of reef-forming melobesioid algae. This debris-facies is very characteristic in the Middle East, and is most typical of the Lower Cretaceous, though known elsewhere from the Upper Jurassic. It occurs much more widely than remains of the littoral deposits where the algal material originated.

A completely different facies prevailed in the Upper Cretaceous of Northern Iraq. Here massive limestones, of reef or shoal and fore-reef facies, with abundant rudist remains, show the largely recrystallized remains of the dasyclad genera *Neomeris* and *Cymopolia*. Presumably these dasyclads grew in quiet situations on and around the reefs and rudist banks. In the Maestrichtian this limestone development tongues eastwards into a clastic facies (transition of Aqra Limestones into Tanjero Formation). As is usual with reef-structures, diagenesis has been active within the main calcareous mass and the best fossils occur at the junction, as with the German Upper Jurassic calcisponge and coral reefs, and the Kurdistan Maestrichtian dasyclad *Cymopolia anadyomenea* was described from this well-preserved marginal material. Within the Tanjero itself two fragmentary algae occur not infrequently ; the dasyclad *Trinocladus radoicicae* and the codiacid *Ovulites delicatula*, represented respectively by rare broken tubes and not uncommon bead-like segments. These are remains of littoral algae, sedimented not far off-shore with the sand-grains, and very similar to, say, the codiacid *Penicillus* and the dasyclad *Batophora* in the Recent Bahamas (Newell *et al.*, 1959 : 224).

Finally, the environments of the Palaeocene Dasycladaceae must be considered.

In Iraqi Kurdistan the fossils occur in two principal intergrading formations of the same age. These are the Sinjar limestones and marls, with a rich and varied dasyclad and other algal flora, and the Kolosh clastics, a coarse green-rock sand with a much more restricted flora of which only two species, only one a dasyclad, are common. Van Bellen (1959) considered the Sinjar as marking the reef-like facies of the Palaeocene (and Lower Eocene), which occurred to seaward of the near-shore Kolosh accumulation-zone of clastic detritus from the land. The Sinjar reefs and shoals did not form a continuous barrier, but a broken line of separate reef-banks and islands, sometimes backed by developments of the lagoonal Khurmala Formation, whose altered deposits sometimes contain indeterminate algal debris.

The Kolosh has yielded occasional examples of such dasyclads as *Cymopolia* and *Dissocladella*, and the codiacid *Halimeda*, etc., but the only common algae are the dasyclad *Trinocladus perplexus* and the codiacid *Ovulites morelleti*. These are presumably the descendants of the species-pair of the same genera recorded above for the lithologically similar underlying Cretaceous Tanjero, but they are much more abundant in the succeeding Kolosh. Presumably they were littoral algae from the coast : some indirect support for this is found in the complete absence of *Trinocladus* from the Sinjar, although *Ovulites* is common there. I would suggest this as possibly evidence that *Trinocladus* for some reason only grew along the coast, whence its broken tubes were wafted into the sandy offshore sedimentation, and that Sinjar shoal-conditions were unfavourable to it. By inference, the bulk of Kolosh fossils of *Ovulites* came likewise from the coastal population, and only a minority from the Sinjar shoals : no more in fact than the odd Kolosh *Cymopolia* etc. (unless indeed these came from a minority population on the coast).

Possibly *Trinocladus perplexus* was restricted to littoral waters with fresh-water dilution from the land drainage : *Teredo*-bored wood is not uncommon in the Kolosh Formation (Elliott 1963b), and this is a familiar indication of adjacent coastal or estuarine conditions, as in the English Lower Eocene London Clay.

The richer Sinjar flora seems to have been buried where it lived, more or less, amongst the pockets, pools and channels of the shoal and reef belt. Sedimentation here was more varied and irregular, and fossils are sporadically more abundant. In submerged channels and on submerged shoals, and in sheltered waters between and to the landward of the barrier-components, the dasyclads found conditions congenial to them : they are often very well-preserved and seem to have been buried where they grew, although rolled and broken material is also not uncommon. In these happy conditions a considerable variety of algae grew together : the last abundance of endospore dasyclads (*Trinocladus*, *Dissocladella*, *Thyrsoporella*) and the rare *Broeckella* co-existing with choristospore genera (*Indopolia*, *Cymopolia*), together with *Clypeina* and the more problematic *Furcoporella*. Codiaceae were represented by abundant *Ovulites*, an extinct relation of the modern *Penicillus*, and by *Halimeda*, not yet swamping the flora. But also in the Sinjar environment was a rich variety of calcareous red algae : melobesioids such as *Archaeolithothamnium* spp., *Lithophyllum*, *Mesophyllum*, *Lithothamnium* and *Lithoporella*, with surviving solenoporoids (*Parachaetetes* and *Solenomeris*), and the problematic *Pseudolithothamnium*

and *Distichoplax*. Most of these were nodular or crusting forms, forming an appreciable volume of the actual reef-structures and plastering the reef-fronts in the surf zone. These two different environments, favoured by the green and red algae respectively, are strikingly demonstrated by an analysis of Palaeocene–Lower Eocene algae from Iraqi Kurdistan. Of 92 samples selected as showing well-preserved algae, from localities all along the mountain arc from Banik in the north to Sirwan-Balambo in the east, 67% show green algae only, 29% red algae only, and only 4% a mixture of the two. Moreover, in the mixed samples one or other group was a worn minority in each case. The preponderance of green-algal, back-reef samples is perhaps to be explained by the inclusion of samples from intertonguing Kolosh Formation, where only green algae occur, but there is no doubt in which environment any particular sample originated. At some localities, e.g. Sirwan-Balambo, red and green algal samples alternate, reflecting the former shifting reef and shoal pattern through time at the spot now arbitrarily revealed as a cliff-section; at others, e.g. Koi Sanjak and Kashti, green and red algae predominate respectively. These differences reflect local aspects of a palaeogeography not known in detail, but emphasize the mutual exclusiveness of the two environments.

In southwestern Iraq the desert outcrops of the Palaeocene Umm er Rhudhama Formation reveal a different picture. This was a more gently-sloping, non-orogenic shore of the Tethys than the opposite coast described above for Kurdistan : the sea extended as a shallow sheet of water on to the slopes of the Arabian landmass, and sedimentation was slow. The algae are abundant ; although abominably ill-preserved, almost all are dasyclads, and there are no red algae at all. This was a shallow-water coast with frequent sheltered bays with limy bottoms on which spreads and thickets of dasyclads proliferated : it is a much less rich flora than that of Kurdistan, and presumably provided few micro-environments like those of the Kurdistan shoal-belt.

Summarizing, with Dasycladaceae especially in mind, the principal kinds of marine algal associations in the Middle East Tethyan rocks examined indicate :

1. Reef and shoal environments, mostly exposed to rough surface water, or tide- or current-swept. The home of nodular or crusting algae (Solenoporaceae, Corallinaceae and the problematic *Lithocodium*), with dasyclads extremely rare.

2. Fore-reef or seaward shoal-slope deposits. Much debris from the environments of category 1, as well as some indigenous non-dasycladacean algae, and only exceptionally dasyclad debris from elsewhere, depending on current-patterns and sediment-transport.

3. Calm lagoonal waters behind reefs and similar barriers. Abundant Dasycladaceae and Codiaceae, few other calcareous algae, with burial on the site of growth, and only exceptionally current-transport to category 2.

4. Calm coastal bays and similar shallow, largely land-locked waters. Dasycladaceae and Codiaceae as in category 3. Burial on the site of growth, occasional current transport to category 2, and much contribution to category 5.

5. Neritic deposits out to sea on coastal shelves. Much sedimentation of broken littoral and sublittoral algal skeletal remains, largely dasycladacean, as a con-

spicuous minority-constituent of calcareous muds. This is the "debris-facies" (Elliott 1958a).

It must be emphasized that some of the local rock-facies encountered are not easily recognizable in terms of the environments set out above. Diagenesis has sometimes obscured or obliterated part of the evidence, but above all knowledge of the small-scale lateral facies-changes is insufficient for full interpretation of the ecology of the fossil-assemblages seen in hand-specimens. The original surveys were stratigraphical and structural in intent, and only much later were the algae recognized by me in thin-sections and hand-specimens of others' collecting, and then put aside for this and other studies.

The Middle East dasyclad environments reconstructed above are varied in time and space, and in the nature of the rocks which now entomb the fossil evidence. But it is noteworthy that none have yielded any evidence to suggest to me that the ecological requirements of the dasyclads of the past were essentially different to those of their living descendants.

VII. THE EVOLUTION OF THE DASYCLADACEAE

From the introductory account given above, it will be remembered that the collection of dasyclads from the Middle East which forms the subject of this work was selected from material collected for general stratigraphical purposes. Exceptionally it proved rich in species for palaeobotanical study, but much of it yielded only sufficient evidence for identification and age-correlation with species previously described elsewhere. Nevertheless, so much material, dasyclad remains from an Upper Palaeozoic to Lower Tertiary timespan in a mid-Tethyan area favourable to them, inevitably invites the question as to whether any further light is thrown on the evolution of the family as a whole.

It may be said at once that nothing emerges seriously to modify the general picture of dasyclad evolution sketched by Julius Pia (Pia, see bibliography of : see also Rezak 1959c). The dasyclads, having achieved the verticillate branch-pattern in the Palaeozoic, proceeded to progressive and varied elaboration of the side-branches, and to the progressive shift of the reproductive structures from within the primitive thick stem-cell, into swollen lateral branches, and finally into special structures borne on the laterals, or into the specialized reproductive discs characteristic of some genera. The reproductive structures themselves are disappointing: they yield no reasonable evidence of sexual mechanisms as have the fossil Melobesioids (e.g. M. Lemoine 1961), or the Chaetangiaceae (Elliott 1961). Presumably the dasyclad reproductive bodies known conventionally in the fossils as sporangia, were similar to those of most Recent genera and so contained resting cysts from which gametes were only set free after shedding : this arose as a necessary consequence of the well-developed calcification around these organs. Release of the reproductive elements thus became only possible after the break-up of the calcified layers, and calcification is usually well-developed around the sporangia. The living *Dasycladus* with restricted stem-cell calcification only, is exceptional in shedding its gametes direct. This condition was regarded by Pia as secondary, *Dasycladus* thus bearing

no more direct relation to the ancestral non-calcified proto-Dasyclad than a naked slug has to the unshelled proto-gastropod. If this is so, and if the present writer's analysis of *Pagodaporella* is correct, then this condition had arisen by the beginning of the Tertiary, but was and is uncommon.

If the fossil sporangia are intrinsically uninteresting, their progressive evolutionary movement within the dasyclad plant, from endospore to cladospore to choristospore, is the most persistent trend in dasyclad evolution. In the genera studied, an endospore genus (*Atractyliopsis*) occurs in the Permian, where it is accompanied by cladospore genera. Cladospore genera predominate in the Mesozoic and survive to the Palaeocene, where they are represented by such genera as *Trinocladus* and *Thyrsoporella*, and *Broeckella*. Choristospore types of conventional pattern appear in the Cretaceous (e.g. *Cymopolia*, which also shows a species intermediate in this character) and are dominant today. In Recent genera with terminal reproductive discs these structures are regarded (Fritsch 1935 : 397 ; Egerod 1952 : 341) as homologous with reproductive structures borne laterally on the primary branches of choristospore dasyclads e.g. *Bornetella*. If the extinct *Clypeina* is grouped with *Acetabularia* and *Acicularia*, as suggested by various workers (see above p. 28), then this specialized condition, expressed in *Clypeina* as serial fertile whorls rather than as a single terminal disc, arose possibly in the Permian, certainly in the Triassic. That is, it arose at the same time as, or later than, the change from endospore to cladospore and before the evolution of the choristospore type proper so far as is known. This suggests that the serial reproductive discs of *Clypeina* are homologous with the swollen branches of cladospore genera, and that the genus (?Permian, Triassic–Oligocene) is thus an earlier, different, achievement of this structure than the Acetabulareae (?Jurassic, Cretaceous–Recent) show. It is noteworthy that the radial tubules of *Clypeina* spp. do not show the calcified sporangial contents in fossils as do those of *Acicularia* ; that is they correspond in this respect to the normal swollen branches of cladospore genera, which only exceptionally display this condition e.g. *Triploporella*. Moreover, *Clypeina* became extinct in the Tertiary as did other cladospore genera, while the living dasyclad flora, of choristospore genera, includes *Acetabularia* and *Acicularia*. It seems likely, therefore, that the discs of *Clypeina* represent an earlier development in time of the condition seen in *Acetabularia*, morphologically similar but of dissimilar origin ; this is a not uncommon phenomenon in evolution. *Clypeina* is therefore placed in the new tribe Clypeineae, to include forms with reproductive discs considered to be of cladospore origin.

From a strictly morphological point of view, the relegation of *Actinoporella* to the synonymy of the earlier-proposed *Clypeina*, now known to contain a small minority of stellate species somewhat like *Actinoporella*, is a logical proposal. However, the earliest stellate *Clypeina*, the Valanginian *C. marteli* Emberger, is one of a group of varied species appearing after the disappearance of the Upper Jurassic *C. jurassica*, and presumably evolved from it at the time of the terminal Jurassic uplifts and lagunal developments. *Actinoporella* itself co-existed in the Upper Jurassic with *C. jurassica*. Pia's suggestion (1927 : 693) that *Clypeina* arose direct from *Actinoporella* must await understanding of the Permian *Clypeina*, and possible new

Mesozoic records. His interpretation of *Actinoporella* as similar to the Triassic *Oligoporella* but differently calcified is followed here : *Actinoporella* is regarded as a valid genus and left in the Diploporeae.

These problems apart, the evolutionary change in position of dasyclad reproductive structures is the most significant feature of their long history. It has been written (Elliott 1962) " we do not clearly know the special advantage of choristosporic structures, whether a direct one in shedding reproductive elements more easily, or an indirect one in their being produced more freely and lavishly with no greater or even less strain on the metabolism of the plant, but although not properly understood it is a main trend in dasyclad evolution ".

Although no precise elucidation of this point can be offered here, the trend itself, clearly indicated by Pia (1920), has been confirmed by subsequent work including the present study. Whatever its significance, it has not saved the Dasycladaceae from decline to a very subordinate position indeed in modern marine floras. Although growths of living dasyclads sometimes form extensive patches or thickets on the sea-floor, I know of no existing deposit in which a great thickness of sediment consisting principally of their calcareous tubes is being accumulated. A prolonged and persistent dense growth of dasyclads to build up considerable thicknesses of dasyclad limestones as are known from the Alpine Trias, e.g. the Essino Limestone of northern Italy, is apparently a thing of the past. Pia (1920 : 187) attributed this decline of the dasyclads principally to the development and spread of the articulated Corallinaceae, with different cellular organization, from the Cretaceous onwards. Much of this spread was into environments for which the dasyclads were not suited, by reason either of the mechanical effects of water movement or of lower temperatures. The appropriate modern ecological analogue comes from a related family of green algae, the Codiaceae, where *Halimeda* occurs in dense growths, notably in the lagoons of atolls and other back-reef environments once largely colonized by dasyclads. Calcified segments from generation after generation of plants pack down to form true *Halimeda*-limestones, well evidenced by borings into the reefs of these

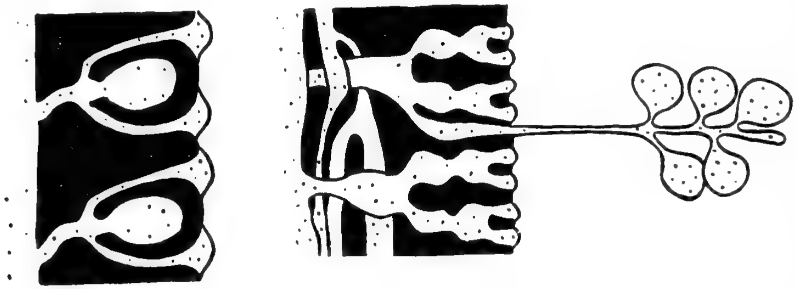


Fig. 15. Diagrammatic vertical sections of comparable portions of the dasyclad *Cymopolia* (left) and the codiacean *Halimeda* (right). Plant tissue stippled, calcareous structure black. To show the encased dasyclad sporangia and free codiacean reproductive growth. Greatly enlarged.

islands, and by many records of *Halimeda*-limestones in the Tertiary of tropical and subtropical latitudes. Since *Halimeda* is quite heavily calcified, it is not calcification itself which has impeded the spread of dasyclads amongst more numerous non-calcified green algae in suitable environments. The explanation probably lies in the reproductive mechanism : *Halimeda* sheds abundant gametes freely from special deciduous non-calcified outgrowths from the segments. In almost all dasyclads the release of the resting cysts depends on eventual break-up of the calcareous structures. The reproductive bodies of *Halimeda* are almost unknown in a fossil state, a unique occurrence being recorded by Pfender (1940 : 245), whereas those of dasyclads survive unbroken in a majority of the specimens found fossil. There is some evidence which has been interpreted as indicating that *Halimeda* was of hybrid codiacean origin in the late Cretaceous (Elliott 1965b) ; certainly its spread and abundance in the Tertiary and at the present day is remarkable. For all their morphological elaboration, the dasyclads did not overcome the initial handicap inherent in the calcification of the reproductive bodies ; this in turn springs indirectly from the basic morphology of laterally whorled stem-cell, the Codiaceae by contrast being formed of richly-branched, agglomerated threads with largely marginal calcification between these and not encasing them, at any rate in the actively growing segments. There is some similarity with marine invertebrate evolution, where, amongst the brachiopods, progressive evolution of very complicated calcareous supports for the fleshy lophophore did not compensate for the basic inferiority of this organ when compared with the functionally comparable gill of the lamellibranch mollusca.

It is difficult, and perhaps impossible, to effect a quantitative consideration of the factors considered above, but they are considered to be in some measure responsible for the " relict group " nature of existing dasyclads, and for their general subordinate position amongst modern marine algal floras.

VIII. REFERENCES

ACCORDI, B. 1956 (preprint issued 1955). Calcareous algae from the Upper Permian of the Dolomites (Italy), with stratigraphy of the " Bellerophon-zone ". *J. palaeont. Soc. India*, Lucknow, **1** : 75–84, pls. 6–12.

ALTH, A. 1878. O galicyjskich gatunkach skamienialych otwornic rodzaju *Gyroporella* Gümb. *Rozpr. Akad. Umiejet*, Krakow, **5** : 71–112, pls. 6–7.

—— 1881–82. Die Versteinerungen des Nizniower Kalksteines. *Beitr. Paläont. Geol. Öst.-Ung.*, Vienna, **1** : 183–332, pls. 18–29.

ANDRUSOV, D. 1939. Rôle des Thallophytes dans la constitution des roches sédimentaires des Carpathes tchécoslovaques. *Mém. Soc. r. Sci. Bohème*, Prague, **1938,** no. 11 : 1–32, 6 pls.

D'ARCHIAC, E. J. 1843. Description géologique du département de l'Aisne. *Mém. Soc. géol. Fr.*, Paris, (1) **5** : 129–418, pls. 24–31, map.

BARTENSTEIN, H. 1965. Unter-Valanginien oder Berriasien : eine Stellungnahme. *Spis. bulg. geol. Druzh.* Sofia, **26** : 51–58.

BARTHOUX, J. 1920. L'Éocène des environs de Suez. *C. r. somm. Séanc. Soc. géol. Fr.* Paris, **1920** no. 10 : 104–105.

BEBOUT, D. G. & COOGAN, A. H. 1964. Algal genus *Anthracoporella* Pia. *J. Paleont.* Chicago, **38** : 1093–96, pl. 169.

BELLEN, R. C. VAN. 1959. "Tertiary", in *Lexique Stratigraphique International* Paris, **3** (Asie), fasc. 10a (Iraq).

BERGGREN, W. A. 1964. The Maestrichtian, Danian and Montian Stages and the Cretaceous-Tertiary Boundary. *Stockh. Contr. Geol.* Stockholm, **11** : 103–176.

BEYDOUN, Z. R. 1960. Synopsis of the Geology of the East Aden Protectorate. *Rept. 21st Int. geol. Congr.* (Norden 1960), **21** : 131–149. (See also the full account in Beydoun 1964).

—— 1964. The Stratigraphy and Structure of the Eastern Aden Protectorate. *Overseas Geol. Miner. Resour. Bull.* London, Suppl. **5** : 1–107, pls. 1–16, maps.

BILGÜTAY, U. 1959. The Permian calcareous algae from south-eastern Anatolia. *Bull. Miner. Res. Explor. Inst.* Ankara, **52** : 48–58, pls. 1–4.

BRACHET, J. L. A. 1965. *Acetabularia*. Endeavour, **24** : 155–161.

BURI, C. Z. 1965. A new Permian *Epimastopora* (Calcareous Alga) from Hunza Valley (Western Karakorum). *Sci. Rep. Ital. Exp.* Karakorum, **4** : 79–88, pls. 8, 9.

CAROZZI, A. 1946. Sur quelques Dasycladacées du Purbeckien du Jura. *C.r. Séanc. Soc. Phys. Hist. nat. Genève*, **63** : 24–26.

—— 1947. La microflore du Purbeckien du Jura suisse. *C.r. Séanc. Soc. Phys. Hist. nat. Genève*, **64**, 13–15.

—— 1948. Étude stratigraphique et micrographique du Purbeckien du Jura Suisse. *Archs Sci. Genève*, **1** : 211–375, pls. 1–6.

—— 1953. Découverte du genre *Salpingoporella* dans le Jurassique supérieur marin du Grand-Salève. *Archs Sci., Genève*, **6** : 382–386.

—— 1954. Survivance du genre *Teutloporella* dans le Jurassique supérieur récifal du Grand-Salève. *Archs Sci., Genève*, **7** : 319–324.

—— 1955a. Dasycladacées du Jurassique supérieur du bassin de Genève. *Eclog. geol. Helv.* Basel, **48** : 31–67, pls. 5, 6.

—— 1955b. Une nouvelle *Griphoporella* dans le Jurassique supérieur et le Crétacé inférieur du domaine jurassien. *Archs Sci.*, Genève. **8** : 203–207.

CASEY, R. 1963. The Dawn of the Cretaceous Period in Britain. *Bull. S.-East. Un. scient. Socs*, London, **117** : 1–15.

CASTRO, P. de. 1962. Il Giura-Lias dei Monti Lattari e dei rilievi ad ovest della Valle dell'Irno e della Piana di Montoro. *Boll. Soc. Nat.* Napoli, **71** : 1–34, pls. 1–19.

—— 1963. Nuove osservazioni sul livello ad *Orbitolina* in Campania. (Note preliminare). *Boll. Soc. Nat.* Napoli, **71** : 103–135, 8 pls.

CHAPMAN, V. J. 1961. *The Marine Algae of Jamaica*. Pt. 1. *Myxophyceae and Chlorophyceae*. Kingston, Jamaica. 159 pp., 176 figs.

CHURCH, A. H. 1895. The structure of the thallus of *Neomeris dumetosa*, Lamour. *Ann. Bot.*, London, **9** : 581–608, pls. 21–23.

CLOUD, P. E. 1952. Facies relationships of organic reefs. *Bull. Am. Ass. Petrol. Geol.*, Chicago, **36** : 2125–49.

COSTANTIN, J. 1920. Sur les siphonées calcaires fossiles de Munier-Chalmas. *C. r. hebd. Séanc. Acad. Sci.*, Paris, **170** : 1028–32.

CUSHMAN, J. A. & GLAZEWSKI, K. 1949. Upper Jurassic Foraminifera from the Nizniow Limestone of Podole, Poland. *Contr. Cushman Lab. foramin. Res.*, Sharon, Mass., **25** : 1–11, pls. 1, 2.

DANGEARD, L. 1931. *Sur la présence de nombreux sporanges de Siphonées verticillées dans les formations colithiques du Jurassique supérieur.* C. r. Congr. Socs sav. Paris Sect. Sci., 64^{e}, Clermont-Ferrand 1931 : 148–49.

DAVIS, A. G. & ELLIOTT, G. F. 1957. The Palaeogeography of the London Clay Sea. *Proc. Geol. Ass.*, London, **68** : 255–277.

DEECKE, W. 1883. Ueber einige neue Siphoneen. *Neues Jb. Miner. Geol. Paläont.*, Stuttgart, Jhrg. **1883 I** : 1–14, pl. 1.

DELMAS, M. & DELOFFRE, R. 1962. Un niveau à algues calcaires au passage Albien-Cénomanien en Aquitaine. *Revue Micropaléont.* Paris, **5** : 214–223, 4 pls.

DERIN, B. & REISS, Z. 1966. *Jurassic microfacies of Israel.* Israel Inst. Petroleum, Spec. Publ. Tel Aviv.

DONZE, P. 1958a. Précisions sur *Clypeina jurassica* Favre. *C. r. somm. Séanc. Soc. géol. Fr.*, Paris, **1958** no. 2 : 21–23.

—— 1958b. Les couches de passage du Jurassique au Crétacé dans le Jura français et sur les pourtours de la " fosse vocontienne ". *Trav. Lab. Géol. Univ. Lyon,* (n.s.), **3** : 1–221.

DOUVILLÉ, H. 1916. Le Crétacé et l'Éocène du Tibet central. *Mem. geol. Surv. India Palaeont indica* Calcutta, n.s. **5** (3) : 1–52, 16 pls.

DUNNINGTON, H. V., WETZEL, R. & MORTON, D. M. 1959. " Mesozoic and Palaeozoic ", in *Lexique Stratigraphique International* Paris, **3** (Asie), fasc. 10a (Iraq).

EDELSTEIN, T. 1964. On the sublittoral algae of the Haifa Bay area. *Vie Milieu* Paris. **15** : 177–210, 2 pls.

EGEROD, L. E. 1952. An analysis of the siphonous Chlorophycophyta. With special reference to the Siphonocladales Siphonales, and Dasycladales of Hawaii. *Univ. Calif. Publs Bot.* Berkeley, **25** : 325–454, pls. 29–42.

ELLIOTT, G. F. 1955a. The Permian calcareous alga *Gymnocodium. Micropaleontology* New York, **1** : 83–90, pls. 1–3.

—— 1955b. Fossil calcareous algae from the Middle East. *Micropaleontology,* New York. **1** : 125–131, 1 pl.

—— 1956. Further records of fossil calcareous algae from the Middle East. *Micropaleontology,* **2** : 327–334.

—— 1957. New calcareous algae from the Arabian Peninsula. *Micropaleontology,* New York. **3** : 227–230, 1 pl.

—— 1958a. Algal debris-facies in the Cretaceous of the Middle East. *Palaeontology,* London. **1** : 254–59, pls. 45–48.

—— 1958b. Fossil microproblematica from the Middle East. *Micropaleontology,* New York. **4** : 419–28, 3 pls.

—— 1959. New calcareous algae from the Cretaceous of Iraq. *Rev. Micropaléont.,* **1** : 217–222, 2 pls.

—— 1960. Fossil calcareous algal floras of the Middle East with a note on a Cretaceous problematicum, *Hensonella cylindrica* gen. et sp. nov. *Q. Jl. geol. Soc. Lond.,* **115** : 217–232, pl. 8.

—— 1961. The sexual organization of Cretaceous *Permocalculus* (calcareous algae). *Palaeontology,* London, **4** : 82–84, pl. 11.

—— 1962a. More microproblematica from the Middle East. *Micropaleontology,* New York, **8** : 29–44, pls. 1–6.

—— 1962b. The distribution of *Broeckella* (calcareous algae) in the Tethyan Palaeocene. *J. geol. Soc. India,* Bangalore, **3** : 49–54.

—— 1963a. Problematical microfossils from the Cretaceous and Palaeocene of the Middle East. *Palaeontology,* London, **6** : 293–300, pls. 46–48.

—— 1963b. A Palaeocene teredinid (Mollusca) from Iraq. *Palaeontology,* London, **6** : 315–17, pls. 51, 52.

—— 1965a. Tertiary solenoporacean algae and the reproductive structures of the Solenoporaceae. *Palaeontology,* London, **7** : 695–702, pls. 104–108.

—— 1965b. The interrelationships of some Cretaceous Codiaceae (calcareous algae). *Palaeontology,* London, **8** : 199–203, pls. 23, 24.

EMBERGER, J. 1956. Les clypéines (algues siphonées verticillées) des Monts des Oulad-Naïl, Atlas saharien, Algérie. *Bull. Soc. géol. Fr.,* Paris, (6) **5** : 543–52, pl. 24.

—— 1957. Aperçu sur la répartition stratigraphique du genre *Clypeina* Michelin. *C. r. somm. Séanc. Soc. géol. Fr.,* Paris, **1957** no. 3, : 45–48.

EMBERGER, J. 1958a. Note préliminaire sur les faciès à algues du Permien du Dj. Tebega (Sud tunisien). *C. r. somm. Séanc. Soc. géol. Fr.*, Paris, **1958** no. 3 : 49–51.

—— 1958b. *Lithoporella elliotti* nov. sp., mélobesiée nouvelle du Jurassique supérieur des monts des Oulad-Naïl, Atlas saharien (Algérie). *Bull. Soc. géol. Fr.*, Paris (6) **7** : 625–29, pl. 32.

EMBERGER, L. 1944. *Les plantes fossiles dans leurs rapports avec les végétaux vivants. (éléments de paléobotanique et de morphologie comparée)*. Paris, 492 pp.

ENDO, R. 1951. Several new species from the Sakamotozawa section, Hikoroichi-mura, Kesen-gun, in the Kitakami Mountain Land. *Trans. Proc. paleont. Soc. Japan, n.s.*, **4** : 121–129.

—— 1953a. Several interesting species from the Kwantô-Mountain Land and a new genus from Kinshôzan, Akasaka, Gifa-ken. *Scient. Rep Saitama Univ.*, (B) **1** : 97–104.

—— 1953b. Stratigraphical and Palaeontological Studies of the Later Palaeozoic Calcareous Algae in Japan, V. *Jap. J. Geol. Geogr.*, **23** : 117–126, pls. 11, 12.

—— 1959. Stratigraphical and paleontological studies of the later Paleozoic calcareous algae in Japan, XIV. Fossil algae from the Nyugawa Valley in the Hida Massif. *Scient. Rep. Saitama Univ.*, Urawa (B) **3** : 177–207, pls. 30–42.

—— 1961. Stratigraphical and paleontological studies of the later Paleozoic calcareous algae in Japan, XV. A restudy of the genus *Epimastopora*. *Scient. Rep. Saitama Univ., Urawa* (B), *Endo Comm.* Vol. : 267–270, pl. 44.

ERK, A. S. & BILGÜTAY, U. 1961. On the occurrence of *Pseudovermiporella* in Turkey. *Bull. geol. Soc. Turkey*, Istanbul, **7** : 108–118, 2 pls.

FAVRE, J. 1932. Présence d'une nouvelle espece d'Algue calcaire siphonée dans le Valanginien du Jura central, *Clypeina inopinata* n. sp. *Eclog. geol. Helv.*, Basel, **25** : 11–16.

FAVRE, J. & RICHARD, A. 1927. Étude du Jurassique supérieur de Pierre-Chatel et de la cluse de la Balme (Jura méridional). *Mém. Soc. Paléont. Suisse*, Geneva, **46** : 39 pp., 3 pls.

FLÜGEL, E. 1966. Algen aus dem Perm der Karnischen Alpen. *Carinthia* II, Klagenfurt, **25** : 1–76, 11 pls., 15 text-figs.

FLÜGEL, H. 1963. Algen und Problematica aus dem Perm Süd-Anatoliens und Irans. *S. B. Akad. Wiss. Wien.*, (1) **172** : 86–95, 2 pls.

FRANCOIS, S., LEHMANN, J.-P., & MAYNC, W. 1958. Sur un niveau à Pseudocyclammines dans le Séquanien du Jura français. *C. r. somm. Séanc. Soc. géol. Fr.*, Paris, **1958** no. 12 : 252–55.

FRITSCH, F. E. 1935. *The Structure and Reproduction of the Algae.* Vol. 1, Cambridge, 791 pp.

GLINZBOECKEL, C. & RABATÉ, J. 1965. *Microfaunes et Microfaciès du Permo-Carbonifère du Sud Tunisien.* Leiden. 45 pp., 108 pls.

GÜMBEL, C. W. 1891. Geognostiche Beschreibung der Frankischen Alb (Frankenjura). *Geogn. Beschr. Konigreichs Bayern*, **4**.

GÜVENC, T. 1965. Etude stratigraphique et micropaléontologique du Carbonifère et du Permien des Taurus occidentaux dans l'arrière—pays d'Alanya (Turquie). *Acad. Thes., Univ. Paris.*

—— 1966a. Presence d'algues calcaires dans le Permien des Taurus occidentaux (Turquie) : description d'un nouveau genre et de quelques espèces. *Rev. Micropaleont.* Paris, **9** : 43–49, 2 pls.

—— 1966b. Description de quelques espèces d'algues calcaires (Gymnocodiacées et Dasycladacées) du Carbonifère et du Permien des Taurus occidentaux (Turquie). *Rev. Micropaléont.*, Paris, **9** : 94–103, pls. 1–3.

HENBEST, L. G. 1963. Biology, mineralogy, and diagenesis of some typical late Paleozoic sedentary foraminifera and algal-foraminiferal colonies. *Cushman Fdn. foramin. Res.* Sharon, Mass., spec. publ. no. **6** : 1–44, 7 pls.

HERAK, M. 1957. Some problems in the dasyclad genus *Diplopora*. *Micropaleontology*, New York, **3** : 49–52.

HILLIS, L. W. 1959. A revision of the genus *Halimeda* (order Siphonales). *Inst. marine Sci., Univ. Texas*, Austin, **6** : 321–403, pls. 1–12.

HUDSON, R. G. S. 1958. Permian corals from northern Iraq. *Palaeontology*, London, **1** : 174–92, pls. 32–35.

—— 1960. The Permian and Trias of the Oman Peninsula, Arabia. *Geol. Mag.*, London, **97** : 299–308, pl. 9.

HUDSON, R. G. S. & CHATTON, M. C. 1959. The Musandam Limestone (Jurassic to Lower Cretaceous) of Oman, Arabia. *Notes Mém. Moyen-Orient*, Paris, **7** : 69–93.

JOHNSON, J. H. 1942. Permian lime-secreting Algae from the Guadalupe Mountains, New Mexico. *Bull. geol. Soc. Am.*, New York, **53** : 195–226, 7 pls.

—— 1951. Permian calcareous algae from the Apache Mountains, Texas. *J. Palaeont.*, Chicago, **25** : 21–30, pls. 6–10.

—— 1954a. An introduction to the study of rock building algae and algal limestones. *Colo. Sch. Min. Quart.*, Golden, **49** (2) : 1–117, 62 pls.

—— 1954b. Cretaceous dasycladaceae from Gillespie county, Texas. *J. Paleont.*, Chicago, **28** : 787–90, pl. 93.

—— 1957. Petrography of the limestones. *In* " Geology of Saipan, Mariana Islands ". *Prof. Pap. U.S. geol. Surv.*, Washington, **280**-C.

—— 1961a. Jurassic algae from the subsurface of the Gulf Coast. *J, Paleont.*, Chicago, **35** : 147–151, pls. 31, 32.

—— 1961b. Limestone-buliding algae and algal limestones. *Publ. Colo. Sch. Min.*, Golden, 297 pp., 139 pls.

—— 1963. Pennsylvanian and Permian algae. *Colo. Sch. Min. Quart.*, Golden, **58** (3) : 211, 81 pls.

—— 1965 Three Lower Cretaceous Algae new to the Americas. *J. Paleont.*, Chicago, **39** : 719–720, pl. 89.

JOHNSON, J. H. & DORR, M. E. 1942. The Permian algal genus *Mizzia*. *J. Paleont.*, Chicago, **16** : 63–77, pls. 9–12.

JOHNSON, J. H. & KASKA, H. V. 1965. Fossil Algae from Guatemala. *Prof. Contr. Colo. Sch. Min.*, Golden, **1** : 152 pp., 47 pls.

KAEVER, M. 1965. Mikropaläontologische Untersuchungen zur Stratigraphie Afghanistans. *Erdöl Kohle Erdgas Petrochem.*, Berlin, **18** : 678–684.

KAMPTNER, E. 1958. Über das System und die Stammesgeschichte der Dasycladaceen (Siphoneae verticillatae). *Annln naturh. Mus. Wien*, **62** : 95–122.

KEIJZER, F. G. 1945. Outline of the geology of the eastern part of the province of Oriente, Cuba. *Geogr. geol. Meded.*, Utrecht, (2), **6** : 1–238, 11 pls., map.

KERCMAR, D. 1962. The first findings of the Upper Jurassic calcareous algae in Slovenia. *Razpr. Geol. Poročila*, Ljubljana, **7** : 9–24, pls. 1–4.

KOCHANSKY, V. & HERAK, M. 1960. On the Carboniferous and Permian Dasycladaceae of Jugoslavia. *Geološki Vjesn.*, Zagreb, **13** : 65–94, pls. 1–9.

KONISHI, K. 1956. *Anatolipora*, a new dasycladacean genus, and its algal associates from the Lower Carboniferous of Japan. *Colo. Sch. Min. Quart.*, Golden, **51** (4) : 109–127, 3 pls.

—— 1961. Studies of Paleozoic Codiaceae and allied genera. Part 1 : Codiaceae (excluding systematic descriptions). *Scient. Rep. Kanazawa Univ.*, Kanazawa, **7** : 159–261, 39 figs.

KONISHI, K. & EPIS, R. C. 1962. Some early Cretaceous calcareous algae from Cochise County, Arizona. *Micropaleontology*, New York, **8** : 67–76, pl. 1.

KÜHN, O. 1933. Das Becken von Isfahan-Saidabad und seine altmiocäne Korallenfauna. *Palaeontographica*, Stuttgart, 79**A** : 143–221, pls. 17–19.

LEBOUCHÉ, M.-C. et LEMOINE, M. 1963. Dasycladacées nouvelles du Lias calcaire (Lotharingien) du Languedoc méditerranéen (St. Chinian, Boutenac). *Rev. Micropaléont.*, Paris, **6** : 89–101, 3 pls.

LEMOINE, M. 1961. Remarques sur la reproduction sexuée des *Archaeolithothamnium*. *Bull. Soc. phycol. Fr.*, Paris, **1961** no. 7 : 8–9.

LLOYD, A. J. 1963. Fusulinids from the Zinnar Formation (Lower Permian) of northern Iraq. *J. Paleont.*, Chicago, **37** : 889–899, pls. 116–120.

LORENZ, T. 1902. Geologische Studien im Grenzgebiete zwischen helvetischer und ostalpinen Facies. II. Der südliche Rhaetikon. *Ber. naturf. Ges. Freiburg. i Br.*, **12** : 34–62, 9 pls.

MASLOV, V. P. 1956. (Fossil calcareous algae of the U.S.S.R.). *Trudy Inst. geol. Nauk*, Moscow, **160** : 1–301, 86 pls.

MASSIEUX, M. 1966a. Présence *d'Ovulites* dans le " calcaire Ypresien " des Corbières septentrionales et discussion sur la nature de l'algue *Griphoporella arabica* Pfender. *Rev. Micropaléont.*, Paris, **8** : 240–248, pls. 1, 2.

—— 1966b. Texte de Juliette Pfender (1940) revu et complété par M. Massieux (avec planches). Première partie. *Rev. Micropaléont.*, Paris, **9** : 111–132, 6 figs., 5 pls. Deuxième partie. Étude critique. *Ibid.* : 135–146, 3 pl.

MAYNC, W. 1966. Microbiostratigraphy of the Jurassic of Israel. *Bull. Israel geol. Surv.*, **40** : 1–56, 10 pls.

MICHELIN, H. 1840–47. *Iconographie Zoophytologique ; description par localités et terrains des polypiers fossiles de France et pays environments.* Paris, 348 pp., 79 pls.

MILANOVIĆ, M. 1965. *Salopekiella*, a new genus of the dasycladaceae family from the Permian sediments of the Velebit Range. *Acta geol. jugoslav. Akad.*, **5** : 373–382, 3 pls.

—— 1966. *Likanella*—a new Permian genus of the family Dasycladaceae. *Geološki Vjesn.*, Zagreb, **19** : 9–14, pls. 1–4.

MORELLET, J. 1951. Contribution à l'étude de *Clypeina jurassica* J. Favre (algue siphonée calcaire), d'après des remarquables échantillons du Jurassique d'Algérie. *Bull. Soc. géol. Fr.*, Paris (5) **20** : 399–402, pl. 22.

MORELLET, L. 1908. Deux algues siphonées verticillées du Thanetien de Boncourt (Oise). *Bull. Soc. géol. Fr.*, Paris (4) **8** : 96–99.

—— 1916. *Note sur les algues siphonées verticillées.* Pp. 47–49 in H. Douvillé (1916).

MORELLET, L. & J. 1913. Les dasycladacées du tertiaire parisien. *Mém. Soc. géol. Fr.*, Paris (paléont.) **47** : 1–43, 3 pls.

—— 1918. Observations sur le genre *Clypeina* Michelin. *Bull. Soc. géol. Fr.*, Paris (4) **18** : 102–05.

—— 1922. Nouvelle contribution à l'étude des dasycladacées tertiaires. *Mém. Soc. géol Fr.*, Paris (paléont.) **58** : 1–35, 2 pls.

—— 1939. *Tertiary siphoneous algae in the W. K. Parker collection, with descriptions of some Eocene siphoneae from England.* Brit. Mus. (Nat. Hist.), London, 55 pp., 6 pls.

—— 1940. Les dasycladacées et les codiacées (algues vertes) du " Calcaire pisolithique ". *C. r. somm. Séanc. Soc. géol. Fr.*, Paris, **1940** no. 11 : 116–118.

MORTON, D. M. 1959. The geology of Oman. *Proc. 5th Wld Petrol. Congr.*, **1** : 277–294.

MUNIER-CHALMAS, E. P. 1877. Observations sur les algues calcaires appartenant au groupe des siphonées verticillées (Dasycladées Harv.) et confondues avec les foraminifères. *C. r. hebd. Séanc. Acad. Sci.*, Paris, **85** : 814–17.

—— 1881. Observations sur les algues calcaires confondues avec les foraminifères et appartenant au groupe des siphonées dichotomes. *Bull. Soc. géol. Fr.*, Paris (3), **7** : 661–670.

NAQIB, K. *et al.* 1960. Geological Observations in the Mizuri Bala area, northern Iraq. *Rept. 21st Int. geol. Congr.* (*Norden* 1960), **18** : 167–181.

NEWELL, N. D. *et al.* 1959. Organism communities and bottom facies, Great Bahama Bank. *Bull. Am. Mus. nat. Hist.*, New York, **117** : 177–228, pls. 58–69.

OTT, E. 1965. *Dissocladella cretica*, eine neue Kalkalge (Dasycladaceae) aus dem Mesozoikum der griechischen Inselwelt und ihre phylogenetischen Beziehungen. *Neues Jb. Miner. Geol. Paläont.*, Stuttgart, Jhrg. **1965** : 683–93.

PANTIĆ, S. 1965. *Clypeina bešići* sp. nov. des sediments triassiques des Dinarides externes. *Bull. géol. Inst. géol. Montenegro*, **4** : 133–141, pls. 1–6.

PARÉJAS, E. & CAROZZI, A. 1953. Une algue marine du genre " *Broeckella* " dans les grès verts du Petit-Salève (Haute-Savoie). *Archs Sci.*, Genève, **6** : 165–171.

PFENDER, J. 1938. Étude micrographique des calcaires Crétacés et Éocènes de l'Imini, de Tamdakht et de Skoura. *Notes Mém. Serv. Mines Carte géol. Maroc*, Rabat, **49** : 57–71, pls. 9–11.

—— 1940. Les algues du Nummulitique égyptien et des terrains Crétacés-Éocènes de quelques regions mésogéennes. *Bull. Inst. Égypte*, **22** : 225–250.

PIA, J. 1918. Thallophyta, pp. 209–222 *in* F. Trauth, Das Eozänvorkommen bei Radstadt im Pongau, usw. *Denkschr. Akad. Wiss.*, Wien, **95** : 171–278, 5 pls.

—— 1920. Die Siphoneae Verticillatae vom Karbon bis zur Kreide. *Abh. zool. bot. Ges. Wien*, **11** (2) : 1–263, 8 pls.

—— 1924. Einige neue oder ungenügend bekannte Siphoneae verticillatae aus dem mitteleuropaïschen Malm. *Annln naturh. Mus. Wien.* **38** : 82–88, 1 pl.

—— 1926. *Pflanzen als Gesteinsbildner.* Berlin. 355 pp., 166 figs.

—— 1927. *Thallophyta* : 1. *Abteilung. In* M. Hirmer "*Handbuch der Paläobotanik*". Munich, Berlin.

—— 1928. Neue Arbeiten über fossile Kalkalgen aus den Familien der Dasycladaceae und Codiaceae (Sammelreferat). *Neues. Jb. Miner. Geol. Paläont.*, Stuttgart, Ref., **1928** III : 227–240.

—— 1930. Upper Triassic fossils from the Burmo-Siamese Frontier. A new Dasycladacea, *Holosporella siamensis* nov. gen., nov. sp., with a description of the allied genus *Aciculella* Pia. *Rec. geol. Surv. India.*, Calcutta, **63** : 177–81, pl. 4.

—— 1932. Remarques sur les algues calcaires. Pp. 13–18, pls. 1–3, in Pia, J., Pfender, J. and Termier, H., "Études géologiques sur les calcaires de Bekrit et de Timhadit (Moyen Atlas)". *Notes Mém. Serv. Mines Carte géol. Maroc.*, Rabat, **20** : 1–18.

—— 1936a. Calcareous green algae from the Upper Cretaceous of Tripoli (North Africa). *J. Paleont.*, Chicago, **10** : 3–13, pls. 1–5.

—— 1936b. Description of the Algae, *in* L. Rama Rao and J. Pia, "Fossil Algae from the uppermost Cretaceous Beds (The Niniyur Group) of the Trichinopoly District, S. India". *Mem. geol. Surv. India Palaeont. indica*, Calcutta, (n.s.) **21** (4) : 49 pp., 6 pls.

—— 1937 Die wichtigsten Kalkalgen des Jungpaläozoikums und ihre geologische Bedeutung. *C. r.* 2^me^ *Congr. Avanc. Ét. strat. Carb.*, **2** : 765–856, pls. 85–97.

PIA, J. Bibliography (by F. Trauth, 1947). *Annln naturh. Mus. Wien*, **55** : 40–49.

PIA, J., RAO, S. R. N. & RAO, K. S. 1937. Dasycladaceen aus Zwischenlagen des Dekkantraps bei Rajahmundry in Südindien. *Sber. Akad. Wiss. Wien*, Abt. 1, **146** : 227–236, pls. 1, 2.

POWERS, R. W. 1962. Arabian Upper Jurassic carbonate reservoir rocks. *Mem. Am. Ass. Petrol. Geol.*, Chicago, **1** : 122–192, pls. 1–7.

PRATURLON, A. 1963a. Dasycladaceae from Upper Permian of the Dolomites. *Geol. romana*, Rome, **2** : 119–137, 5 pls.

—— 1963b. Una nouva *Teutloporella* (alga calcarea) nel Giurese superiore di Monte Corno (Parco Nazionale d'Abruzzo). *Geol. romana*, Rome, **2** : 199–206, 1 pl.

—— 1964 Calcareous algae from Jurassic-Cretaceous Limestone of central Apennines (southern Latium-Abruzzi). *Geol. romana*, Rome, **3** : 171–201, 34 figs.

—— 1966. Algal assemblages from Lias to Paleocene in Southern Latium-Abruzzi : a review. *Boll. Soc. geol. ital.*, Rome, **85** : 167–194, 16 figs.

PUISEUX-DAO, S. 1966. *Siphonales and Siphonocladales.* II. *The Dasycladaceae.* Pp. 59–72 *in* M. B. E. Godward, "*The Chromosomes of the Algae*" London 8vo. 212 pp.

QATAR PETROLEUM COMPANY, Ltd. 1960. *A review of the geological occurrence of oil and gas in Qatar.* Publ. 2nd Arab Petrol. Congr., 10 pp.

RADOIČIĆ, R. 1958. *Munieria baconica* Deecke dans les couches du Crétacé inférieur aux environs de Titograd. *Bull. Serv. géol. geoph. Serbie*, Belgrade, **16** : 79–86, 1 pl.

—— 1959. *Salpingoporella dinarica* nov. sp. dans les sédimentes crétacés inférieurs des Dinarides. *Bull. géol. Inst. géol. Montenegro*, **3** : 33–42, pls. 3–5.

RADOIČIĆ, R. 1960. Microfaciés du Crétacé et du Paléogène des Dinarides externes de Yougoslaves. *Paléontologie des Dinarides Yougoslaves* (A : micropaleont.) Titograd. **4** (1) : 1–172, 67 pls.

—— 1962. Sur une nouvelle Dasycladacée. du Jurassique superiéur, *Pianella grudii* nov. gen., nov. sp. *Bull. Inst. r. Geol. Geof.* (A) **20** : 201–210, 3 pls.

RAINERI, R. 1922. Alghe sifonee fossili della Libia. *Atti. Soc. ital., Sci. nat.*, Palermo, **61** : 72–86, pl. 3.

RAJAGOPALAN, N. 1965. Late Cretaceous and early Tertiary stratigraphy of Pondicherry, South India. *J. geol. Soc. India*, Bangalore, **6** : 108–121.

RAO, S. R. N. & VIMAL, K. P. 1955. Fossil algae from Sind, Pakistan. *Micropaleontology* New York, **1** : 91–92, 1 pl.

REISS, Z. 1961. Lower Cretaceous microfacies and microfossils from Galilee. *Bull. Res. Coun. Israel*, Jerusalem, **10** G : 223–242, 8 pls.

REZAK, R. 1957. Occurrence of *Clypeina* in the Eocene of Florida. *Micropaleontology*, New York, **3** : 281–86, 1 pl.

—— 1959a. New Silurian Dasycladaceae from the southwestern United States. *Colo. Sch. Min. Quart.*, Golden, **54** (1) : 115–29, pls. 1–4.

—— 1959b. Permian algae from Saudi Arabia. *J. Paleont.*, Chicago, **33** : 531–39, pls. 71, 72.

—— 1959c. Paleozoic evolution of the Dasycladaceae. *Proc. 9th Int. Bot. Congr.*, **2** : 325 (Abstr.).

SARTONI, S. & CRESCENTI, U. 1960. La zona a *Palaeodasycladus mediterraneus* (Pia) nel Lias dell'Appennino meridionale. *G. Geol.*, Bologna (2), **27** : 1–25, pls. 1–3.

—— 1962. Ricerche biostratigrafiche nel mesozoico dell' Appennino meridionale. *G. Geol.*, Bologna, (2), **29** : 161–304, pls. 11–52.

SASTRY, M. V. A. & RAO, B. R. J. 1964. Cretaceous-Tertiary boundary in South India. *Rept. 22nd Int. Geol. Congr.* (India 1964), Abstr. **34.**

SCHUBERT, R. J. 1907. Vorläufige Mitteilung über Foraminiferen und Kalkalgen aus dem dalmatinischen Karbon. *Verh. K.K. geol. Reichanst.*, Wien, (1907), 211–214.

—— 1908. Zur Geologie des osterreichischen Velebit. *Jb. K. K. geol. Reichanst.*, Wien, **58** : 345–86, pl. 16.

SCHWAGER, C. 1883. Die Foraminiferen aus den Eocaenablagerungen der libyschen Wüste und Aegyptens. *Palaeontographica*, Stuttgart, **30** (2) Pal. Teil. ref. : 146–47, pl. 29.

SPJELDNAES, N. 1963. A new fossil (*Papillomembrana* sp.) from the Upper Precambrian of Norway. *Nature*, London, 119—200 : 63–64.

STEINMANN, G. 1880. Zur Kenntniss fossiler Kalkalgen (Siphoneen). *Neues Jb. Miner. Geol. Paläont.*, Stuttgart, Jhrg. **1880** II : 130–140, pl. 5.

—— 1899. Ueber fossile Dasycladaceen vom Cerro Escamela, Mexico. *Bot. Ztg.*, Berlin & Leipzig, **57** : 137–154.

SVEDELIUS, N. 1924. On the discontinuous geographical distribution of some tropical and subtropical marine algae. *Ark. Bot.*, Uppsala, **19** (3) : 1–70, 14 figs. (maps).

—— 1953. Critical studies on some species of *Galaxaura* from Hawaii. *Nova Acta R. Soc. Scient. upsal.*, Uppsala, (4) **15** (9) : 1–92, 70 figs.

THIEULOY, J.-P. 1959. Étude micrographique des " calcaires a débris " barremo-aptiens sur le pourtour méridional du Vercors. *Trav. Lab. Géol. Univ. Grenoble*, **35** : 39–99, 25 pls.

VARMA, C. P. 1950. A new genus of calcareous alga (Dasycladaceae) from the Ranikot Beds (Palaeocene) of the Punjab Salt Range. *Curr. Sci.*, Bangalore, **19** : 207–208.

—— 1952. *Clypeina* (Dasycladaceae) from the Cretaceous of South India. *Palaeobotanist*, Lucknow, **1** : 439–41, 1 pl.

—— 1955. Further observations on *Morelletpora nammalensis* Varma from the Khairabad Limestone (Ranikot) Beds of the Nammal Gorge, Punjab Salt Range. *Palaeobotanist* Lucknow, **4** : 101–11, 2 pls.

WALTON, J. 1925. On a calcareous alga belonging to the Triploporelleae (Dasycladaceae) from the Tertiary of India. *Rec. geol. Surv. India*, Calcutta, **56** : 213–219, pl. 16.
WOOD, A. 1940. Two new calcareous algae of the family Dasycladaceae from the Carboniferous Limestone. *Proc. Lpool geol. Ass.*, Liverpool, **18** : 14–18, pl. 2.
—— 1943. The algal nature of the genus *Koninckopora* Lee ; its occurrence in Canada and Western Europe. *Q. Jl. geol. Soc. Lond.*, **98** : 205–222, pls. 8–10.
—— 1964. A new dasycladacean alga, *Nanopora*, from the Lower Carboniferous of England and Kazakhstan. *Palaeontology*, London, **7** : 181–85, pls. 31–32.

IX. APPENDIX

Geographical co-ordinates of localities mentioned in the text.

ABIAD, J.	56°35′E 23°35′N
ADANA	35°18′E 36°58′N
AIDAH	43°40′E 30°50′N approx.
AL GHURRA	43°40′E 30°50′N approx.
AL HAMIAH	47°40′E 14°00′N
ALA-DAG	29°30′E 36°30′N
AMADIA	43°29′E 37°05′N
AQABAR KHEMER	48°12′E 14°48′N
AQRA	43°45′E 36°47′N
ARGOSH	44°10′E 37°8′ N
ARUS, W.	48°20′E 14°15′N
ATSHAN	42°55′E 36°20′N
AWASIL	42°49′E 33°27′N
BALAMBO	45°58′E 35°7′ N
BANIK	42°58′E 37°12′N
BASRAH	47°51′E 30°30′N
BATINAH	56°57′E 24°25′N
BEKHME	44°14′E 36°40′N
BIH, W.	56°10′E 25°45′N
BURUN (BURUM)	49°00′E 14°30′N
BUSYAH, J.	56°10′E 25°45′N
BUWAIDA, J.	56°20′E 23°10′N
CHALKI	43°10′E 37°14′N
CHALKI ISLAM (see Chalki)	
CHAMA	44°14′E 36°50′N
DAMMAM	50°00′E 26°20′N
DIYANA (DIANA)	44°33′E 36°40′N
DIZA	44°18′E 36°46′N
DUKHAN	50°47′E 25°26′N
FAHUD	56°31′E 22°18′N
FAIYAH, J.	55°50′E 25°10′N
FALLUJAH	43°46′E 33°21′N
GAL-I-MAZURKA	43°29′E 37°05′N
GARA, J.	43°27′E 36°59′N
GHABAR	48°45′E 14°13′N
HAGAB, J.	56°10′E 25°45′N
HAJAR, W.	48°00′E 14°30′N
HARUR	43°15′E 37°14′N
HAUSHI	57°40′E 21°00′N
HUGF	57° E 20° N
JOL BA HAWAR	48°18′E 14°25′N
JUWEIZA	55°42′E 25°14′N
KASHTI	45°45′E 35° 8′N
KAUR, J.	58° E 22°30′N
KIRKUK	44°24′E 35°28′N
KOI SANJAK	44°38′E 36° 5′N
LAUT, J.	47°00′E 14°15′N
MA'ADI PASS	49°25′E 15°00′N
MAKHUL	43°20′E 35°13′N
MILEH THARTHAR	42°44′E 32°11′N
MINTAQ	48°00′E 14°30′N
MURBAN	53°44′E 23°53′N
MUSAIYIB	44°25′E 32°49′N
ORA	43°21′E 37°17′N
PILA SPI	45°45′E 35°15′N
QAMAR, J.	56°04′E 25°28′N
RAS SADR	54°44′E 24°48′N
ROWANDUZ	44°33′E 36°37′N
RU KUCHUK	44° 8′E 36°56′N
SAHIL MALEH	58°40′E 23°40′N
SARMORD	45°02′E 35°54′N
SEDELAN	45°00′E 35°45′N
SEKHANIYAN	45°09′E 35°52′N
SIRWAN	46°10′E 35°05′N
SULEMANIA	45°26′E 35°33′N
SUNDUR	43° 4′E 30°56′N
SURDASH	45°06′E 35°51′N
TANAMIR, J.	58°06′E 22°39′N
TAWI SILAIM	58°35′E 22°25′N
WAGSA	43°45′E 30°35′N
ZIBAR-ISUMERAN	44° 5′E 36°52′N

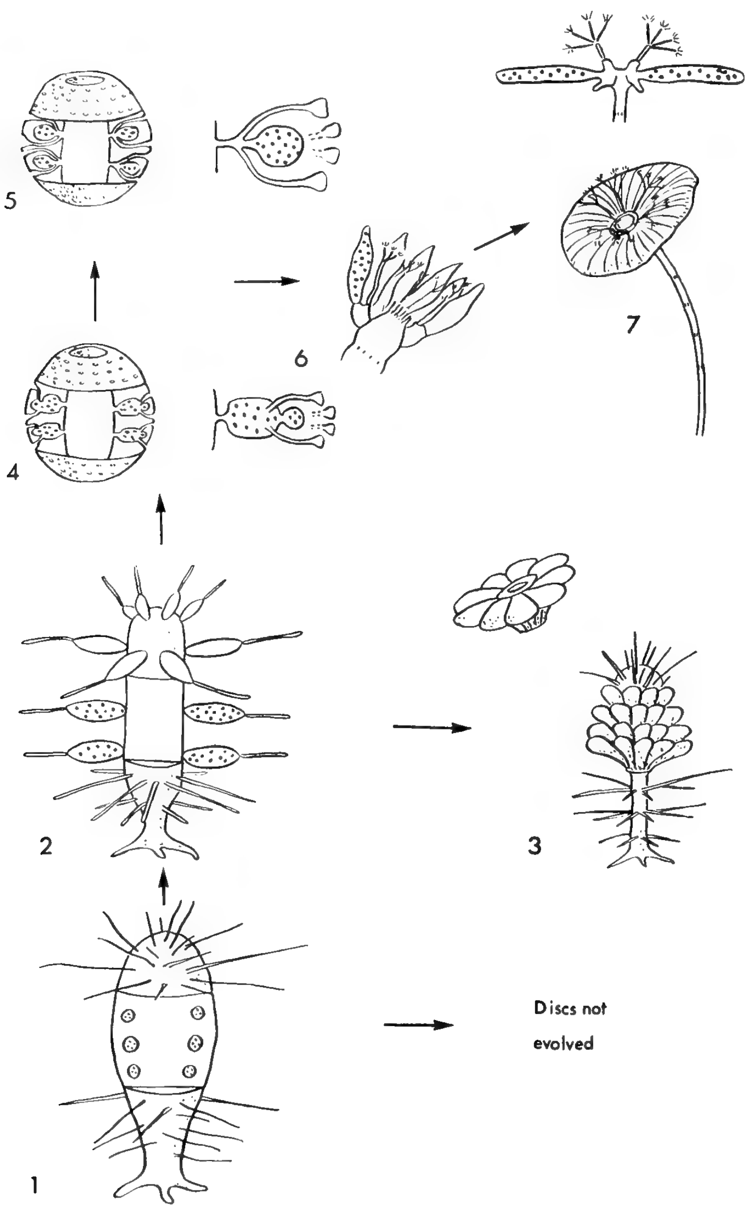


FIG. 16. Reproductive Evolution in Dasycladaceae. 1. Idealized endospore dasyclad (typically Palaeozoic), showing sporangia within the stem-cell and simple, sterile branches. No calcification shown : this feature is variable between different known genera. 2. Idealized cladospore dasyclad (typically Mesozoic), showing sporangia within swollen branches, and separate whorls of fertile and sterile branches. No

EXPLANATION OF PLATES

Unless otherwise stated, all material is housed in the British Museum (Natural History).

---

calcification shown : this feature is variable between different known genera. 3. *Clypeina* : separate fossil disc and reconstruction of living plant (Permian to Oligocene). Separate whorls of naked sterile branches and fertile whorls of fused, heavily-calcified branches. Shape and fusion of discs or cups variable between species. 4. Segment of *Cymopolia eochoristosporica* Elliott (Upper Cretaceous), and separate branch-diagram. This species transitional between cladospore and choristospore, showing as a small cymopoliform branch-system developing on the end of a swollen cladospore branch. 5. Segment of *Cymopolia* sp. (Tertiary) and separate branch-diagram, to show typical choristospore branch with separate sporangial body at junction of primary and secondary branches. *Cymopolia* is segmented and heavily calcified, but other choristospore genera exist which are single (non-segmented) and more lightly calcified. 6. Sketch of portion of *Halicoryne* (Recent) to illustrate choristosporic organization with different proportions and arrangement of the component elements. The large elongate gametangium (left) is paired with a much smaller sterile branch-system, the whole whorl grouped in a loose basket-like circular arrangement. Light incomplete calcification only. 7. *Acetabularia* (Recent). Plant showing typical mature calcified reproductive disc and stem, also diagrammatic cross-section of disc. This may be regarded as a fused calcified structure analogous to that of *Halicoryne* (note small sterile branches) : the scars of early sterile whorls may be seen on the stem. *Acetabularia* is thus the choristosporic disc-analogue to the cladosporic *Clypeina*, as now interpreted.

PLATE 1

Acicularia, Acroporella, Actinoporella, Anthracoporella

FIGS. 1, 3. *Acicularia antiqua* Pia, random cuts in thin-section, ×60. Cretaceous, Barremian-Aptian, Upper Musandam Formation : Jebel Hagab, Oman, Arabia. V. 52031.

FIG. 2. *Actinoporella podolica* Alth, near-vertical section through stem-cell and two branches of one verticil, ×28. Cretaceous, Valanginian, Garagu Formation : Banik, Mosul Liwa, Iraq. V.41630.

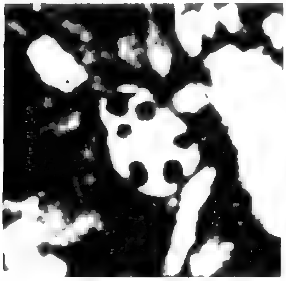
FIG. 4. *A. podolica*, near-horizontal section through a verticil, ×45. Cretaceous, Valanginian-Hauterivian, Sarmord Formation ; Jebel Gara, Mosul Liwa, Iraq. V. 41579.

FIG. 5. *Acroporella assurbanipali* gen. et sp. nov., oblique-vertical section, ×20. Holotype. Cretaceous, Valanginian-Hauterivian, Garagu Formation ; subsurface, Kirkuk Well no. 116. V. 52032.

FIG. 6. *Acicularia* (*Briardina*) sp., thin-section along spicule, ×60. Palaeocene-Lower Eocene ; Sahil Maleh, Batinah Coast, Oman, Arabia. V. 52033.

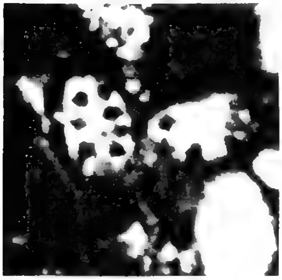
FIG. 7. *A. podolica*, typical random tangential-vertical cut through adjacent radial tubules of verticil, ×30. Cretaceous, Valanginian-Hauterivian, Sarmord Formation ; Jebel Gara, Mosul Liwa, Iraq. V. 52034.

FIG. 8. *Anthracoporella mercurii* sp. nov., thin-section, holotype. Permian, Bih Dolomite ; Wady Bih, Jebel Hagab, Peninsular Oman, Arabia. V. 52035.



1

2

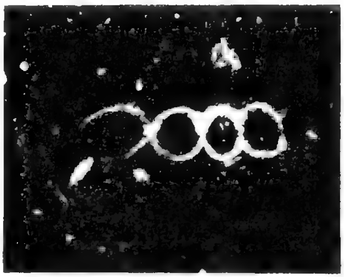


3

4

5

6



7

8

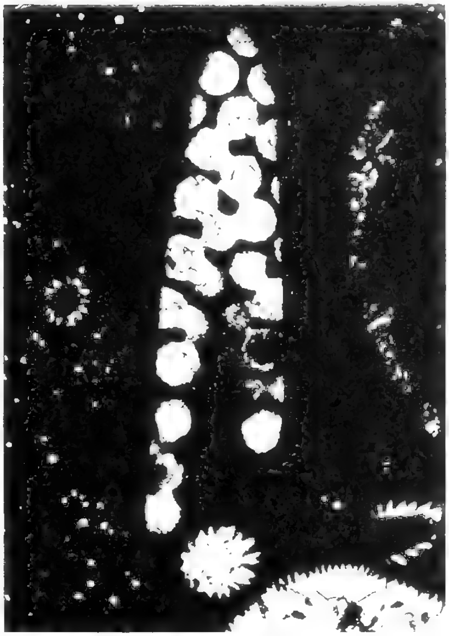
PLATE 2

Anthracoporella, Atractyliopsis

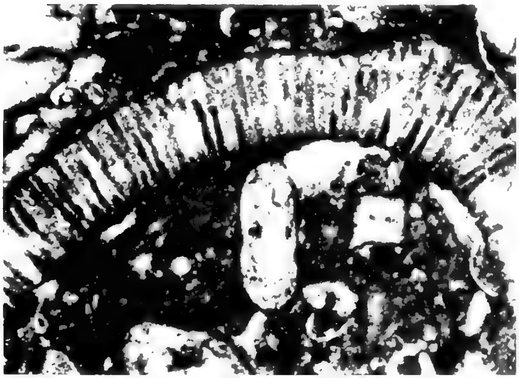
FIGS. 1, 2. *Anthracoporella spectabilis* Pia, thin-section ×12, and portion enlarged to show wall-detail, ×24. Permian ; derived cobble in Triassic conglomerate ; Jebel Busyah, Oman, Arabia. V. 52036.

FIGS. 3–5. *Atractyliopsis darariensis* sp. nov. Thin-sections ; 3. Paratype, oblique-vertical, ×28 V. 52015 ; 4. Paratype, vertical, incomplete example, ×40 V. 52037 ; 5. Holotype, vertical, long gently-curved example, ×20 V. 52037. Upper Permian, Darari Formation; Ora, Mosul Liwa, Iraq.

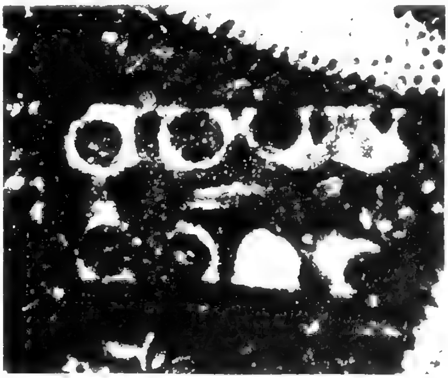
1



3



2



4

5

PLATE 3

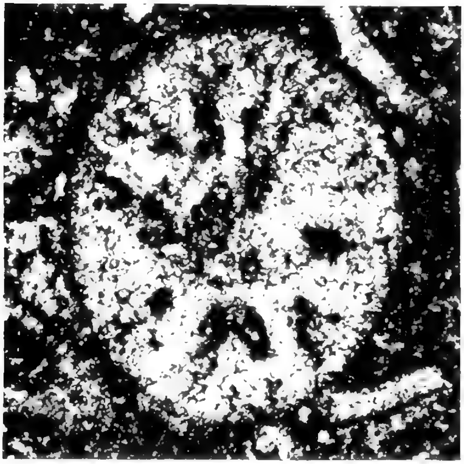
Broeckella, Clypeina

FIG. 1. *Broeckella belgica* Morellet, transverse thin-section, ×50. Palaeocene ; Sahil Maleh, Batinah Coast, Oman, Arabia.

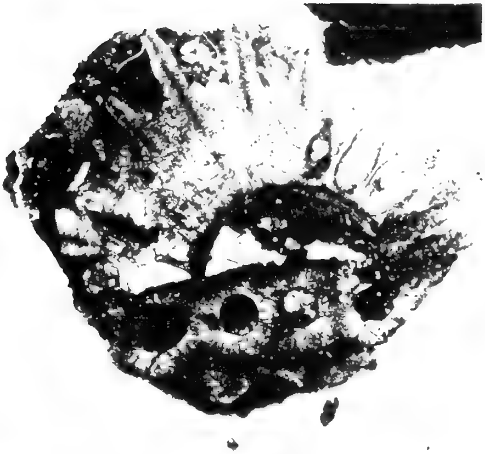
FIGS. 2, 3. *Clypeina jurassica* Favre, thin-sections, ×30. 2. Associated fragments ; above, transverse (horizontal) section of broken verticil, showing radial tubules with example of communicatory pore to stem-cell on right and distinctive thin-section appearance of adjacent tubules in this species at top centre ; below, tangential-vertical cut of thick-walled tubules at about mid-tubule zone radially. V. 52038. 3. Oblique-vertical cut of plant with successive verticils in position ; the plane of section passes from central (below) to obliquely through stem-cell wall and inner tubule-junction (middle) to outer tubules of third verticil. V. 52039. Upper Jurassic, Najmah Formation ; subsurface, Kirkuk Well No. 117, Iraq.

FIG. 4. *C. jurassica*, slightly oblique transverse cut through one verticil, ×30. Upper Jurassic, Arab Zone ; subsurface, Dukhan No. 28 Well, Qatar, Arabia. V. 52040.

FIG. 5. *C. jurassica*, transverse cut through one worn verticil, showing the resistant nature of the calcification at the fusion between adjacent tubules, ×30. Upper Jurassic, Najmah Formation ; subsurface, Kirkuk Well No. 117, Iraq. V. 52041.

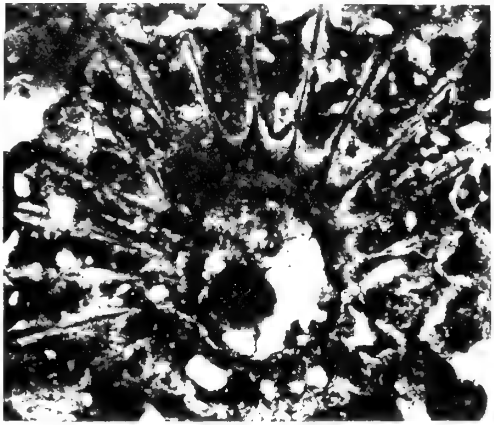


1

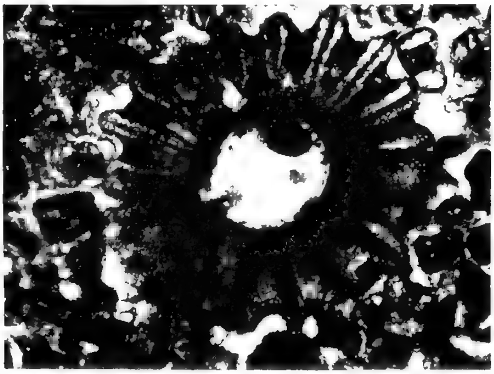


2

3



4



5

PLATE 4

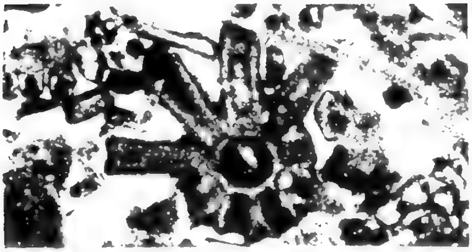
Clypeina

FIG. 1. *Clypeina marteli* Emberger, transverse thin-section, ×28. Cretaceous, Valanginian ; Hugf, Southern Oman, Arabia. V. 52042.

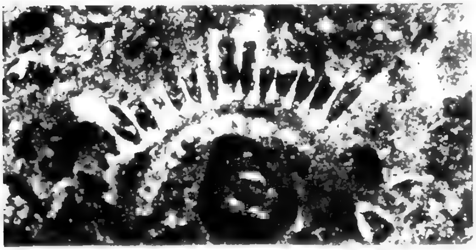
FIG. 2. *Clypeina merienda* Elliott, oblique-transverse thin-section through verticil to show bases of tubules and part of central ring. ×35. Palaeocene, Sinjar Formation ; Koi Sanjak, Erbil Liwa, Iraq. V. 52043.

FIGS. 3, 7, 8. *C. merienda*, thin sections, ×28. Palaeocene, Sinjar Limestone. 3. Transverse cut of broken verticil. Sirwan, Sulemania Liwa, Iraq. V. 41586. 7. Oblique cut of successive verticils. Koi Sanjak, Erbil Liwa, Iraq. V. 52043. 8. Vertical-tangential cut of numerous successive verticils of one plant. Sirwan, Sulemania Liwa, Iraq. V. 41587.

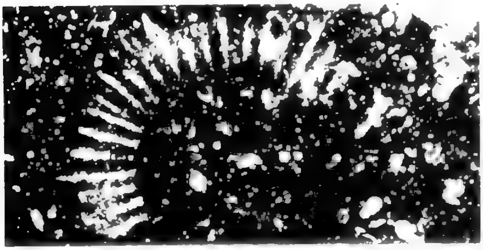
FIGS. 4, 5, 6. *C. jurassica*, solid (dissociated) verticils, showing top, side and bottom appearances, ×28. Upper Jurassic, Arab zone ; subsurface, Dukhan No. 2 Well, Qatar, Arabia. V. 52044, V. 52045, V. 52046.



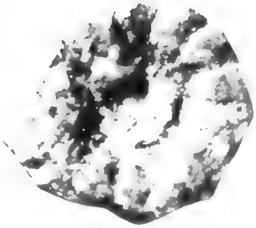
1



2

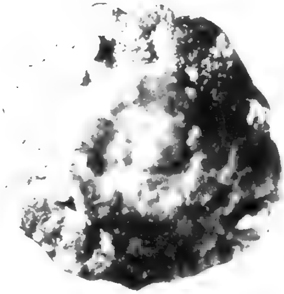


3



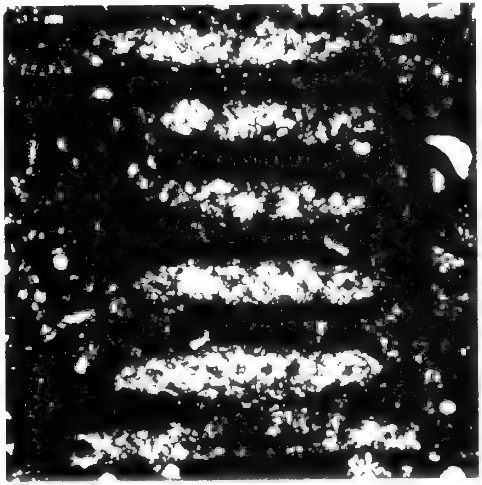
4

5



6

7



8

PLATE 5

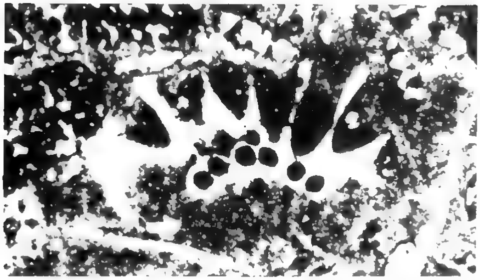
Clypeina

FIGS. 1, 3. *Clypeina* ("*Eoclypeina*") sp., thin-sections of debris, ×40. Permian, basal Satina Formation and top Zinnar Formation respectively ; Harur, Mosul Liwa, Iraq. V. 41598, V. 52048.

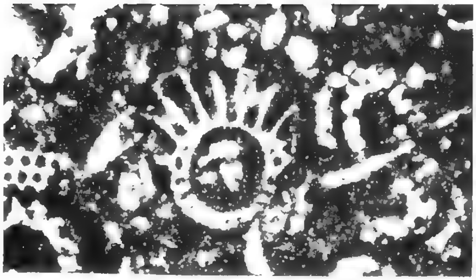
FIG. 2. *Clypeina* sp., slightly oblique-transverse section of verticil, ×30. Palaeocene ; Ghurra Beds, Umm er Radhama Formation ; Al Ghurra, Diwaniya Liwa, Iraq. V. 52047.

FIG. 4. *Clypeina lucasi* Emberger, oblique-transverse section of verticil, ×28. Cretaceous. Valanginian ; Hugf area, Southern Oman, Arabia. V. 52042.

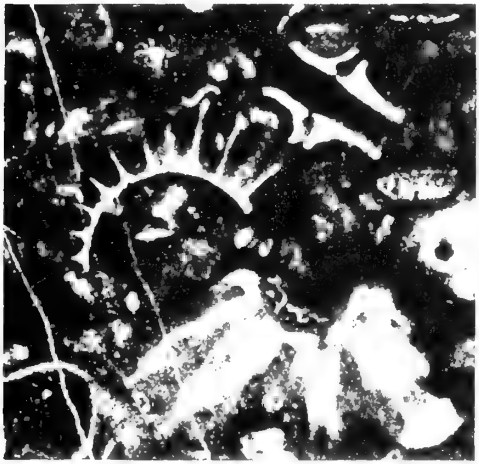
FIGS. 5, 6. *Clypeina parvula* Carozzi, thin-sections showing random transverse and fragmentary longitudinal sections, ×60. Cretaceous, Valanginian, Garagu Formation ; subsurface, Kirkuk Well No. 116, Iraq. V. 52049, V. 52050.



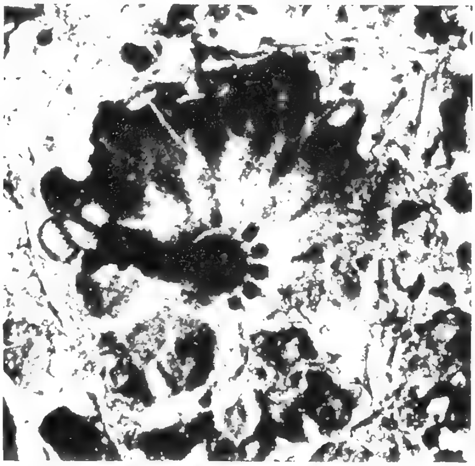
1



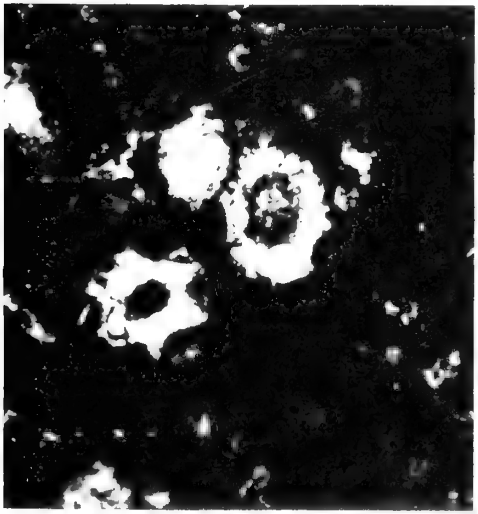
2



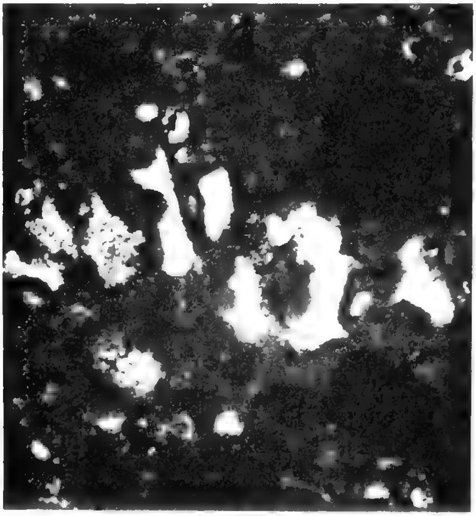
3



4



5



6

PLATE 6

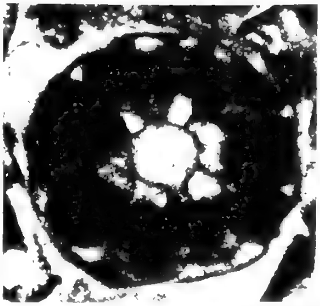
Cylindroporella

FIGS. 1, 2. *Cylindroporella arabica* Elliott, longitudinal and transverse thin-sections, ×58. Upper Jurassic, " Arab Zone " ; subsurface, Dukhan No. 28 Well, Qatar, Arabia. V. 41629.

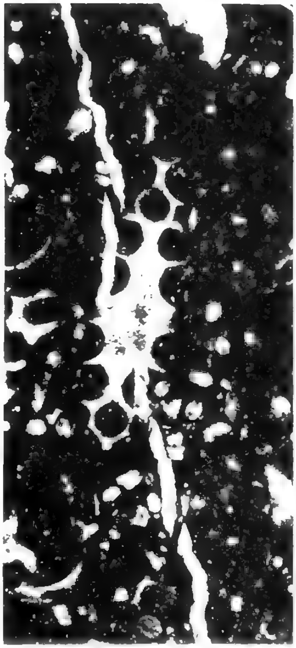
FIGS. 3, 4. *Cylindroporella barnesi* Johnson. 3. Random oblique section, ×30. Cretaceous, Valanginian-Hauterivian, Garagu Formation ; subsurface, Makhul No. 2 Well, Mosul Liwa, Iraq. V. 52051. 4. Random tangential section, ×60. Cretaceous, about Aptian level, Sarmord Formation ; Sekhaniyan, Surdash, Sulemania Liwa, Iraq. V. 52052.

FIGS. 5–7. *Cylindroporella sugdeni* Elliott. 5. Longitudinal section, ×35. V. 52053. 6. Transverse section, ×28. V. 41623. 7. Tangential section, ×28. V. 41620. Lower Cretaceous ; subsurface, Fahud No. 1 Well, Oman, Arabia.

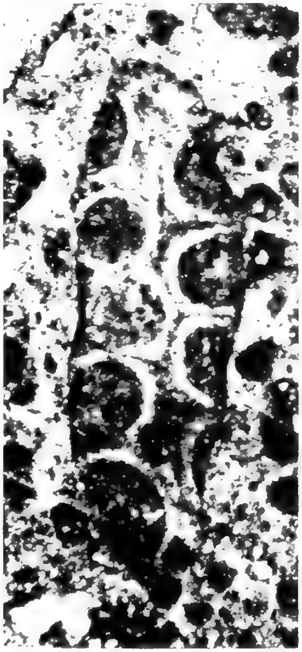
1



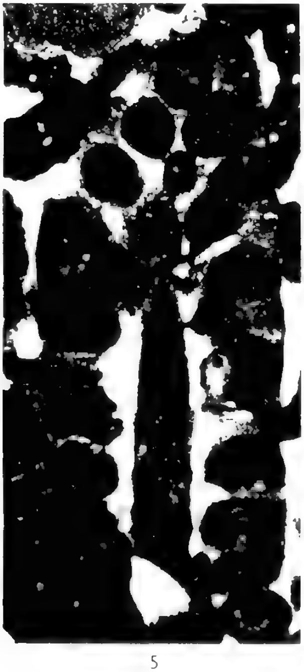
2



3

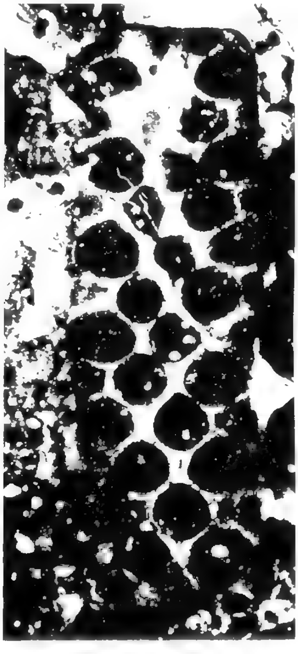


4



5

6



7

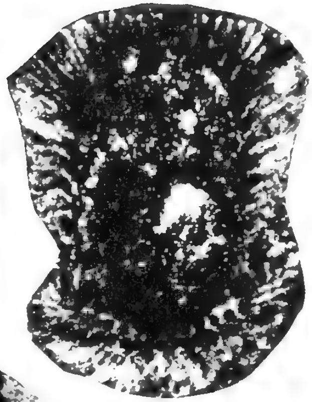
PLATE 7

Cymopolia

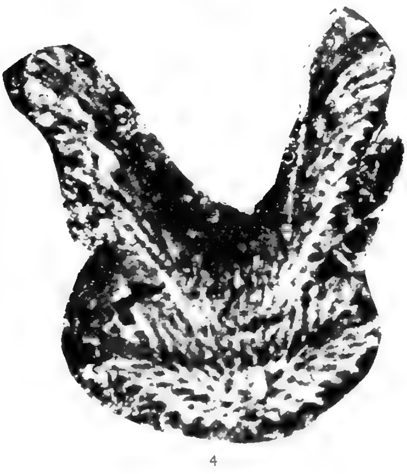
FIGS. 1–5. *Cymopolia anadyomenea* Elliott. 1. Longitudinal section, ×28. V. 41656. 2. Transverse section, ×28. V. 41656. 3, 4. Oblique sections, ×28. V. 41656, V. 41655. 5. Solid specimen on weathered surface, ×20. V. 52054. Cretaceous, Maestrichtian, Tanjero Formation ; Diza North, Erbil Liwa, Iraq.

1

2



3



4

5

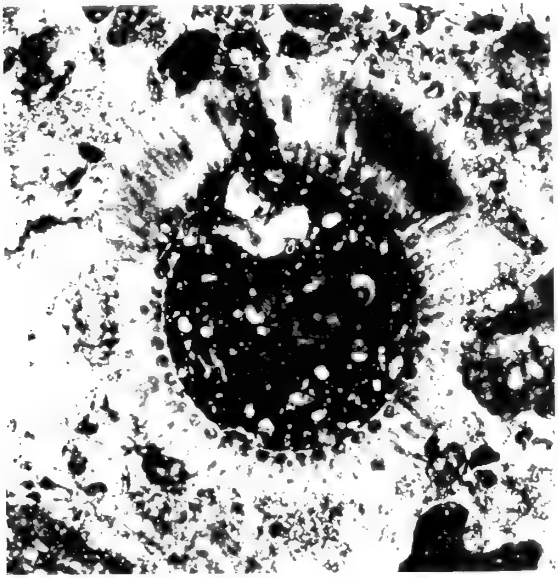
PLATE 8

Cymopolia

FIGS. 1, 5. *Cymopolia anadyomenea* Elliott. 1. Oblique-transverse section, ×28. Cretaceous, Maestrichtian, Tanjero Formaton ; Diza North, Erbil Liwa, Iraq. V. 52055. 5. Debris, in limestone facies, thin-section ×20. Cretaceous, Maestrichtian, Upper Aqra Formation ; Aqra, Mosul Liwa, Iraq. V. 52056.

FIG. 2. *Cymopolia barberae* sp. nov., holotype, transverse thin-section, ×50. Palaeocene-Lower Eocene, Kolosh Formation ; Surdash, Sulamenia Liwa, Iraq. V. 52057.

FIGS. 3, 4. *Cymopolia tibetica* Morellet. 3. Transverse section, ×60. Cretaceous, Maestrichtian, Aqra Formation ; Aqra, Mosul Liwa, Iraq. V. 52059. 4. Fragment to show branch-structure, thin-section, ×60. Cretaceous, Maestrichtian, Aqra-Hadiena Limestone Facies ; Chalki Islam, Mosul Liwa, Iraq. V. 52060.



1

2

3

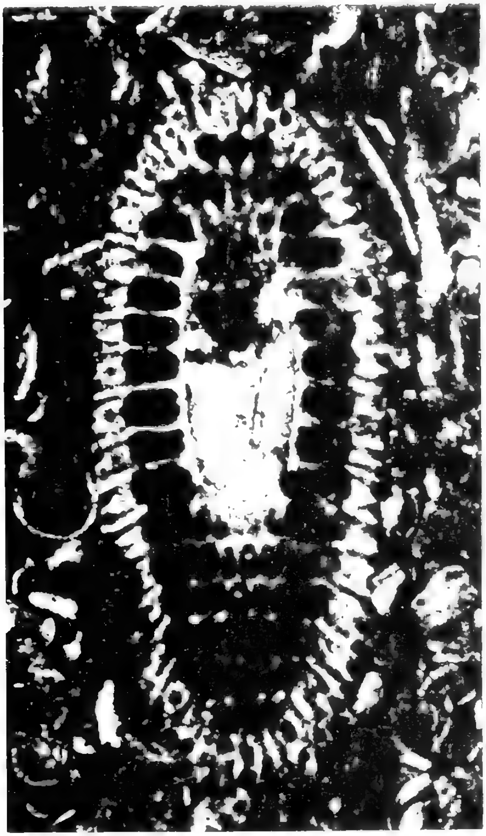
4

5

PLATE 9

Cymopolia

FIGS. 1–3. *Cymopolia eochoristosporica* sp. nov. 1. Oblique-longitudinal thin-section, ×20. Holotype, V. 52652. 2. The same, to show branch and sporangial-detail, ×40. 3. Another oblique-longitudinal thin-section, portion ×40. Syntype, V. 52653. Both from Cretaceous, Maestrichtian, subsurface Aruma Formation ; Murban No. 53 Well, Abu Dhabi, Trucial Oman, Arabia.



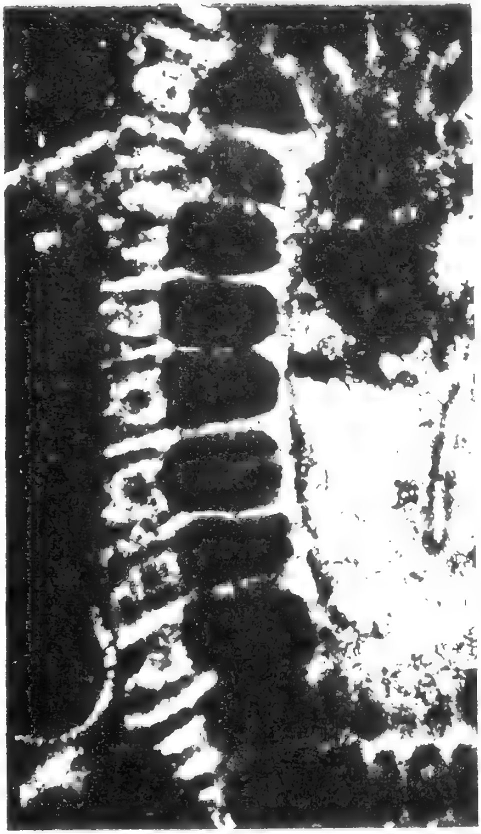


PLATE 10

Cymopolia, Dissocladella

FIG. 1. *Cymopolia elongata* (Defrance) Mun.-Chalmas. Solid specimen, small single unit or segment, ×28, for comparison of external pores (branch-openings) with those of *C. kurdistanensis* (fig. 2). Eocene, Lutetian ; Grignon, Paris, France. V. 52061.

FIGS. 2–5. *Cymopolia kurdistanensis* Elliott. 2. Solid specimen, single segment, to show detail of exterior, ×28. Palaeocene-Lower Eocene, Kolosh Formation, Bekhme, Erbil Liwa, Iraq. V. 52062. 3. Thin-section of dissociated segment, to show details of sporangia and branches, ×28. Palaeocene, Sinjar Formation ; Banik, Mosul Liwa, Iraq. V. 41593. 4. Slightly oblique transverse cut showing sporangia and branches, ×36. Palaeocene, Kolosh Formation ; Rowanduz, Erbil Liwa, Iraq. V. 52063. 5. Random transverse section at an inter-sporangial level so that only the branches are seen, ×30. Palaeocene ; Jebel Faiyah, Trucial Oman, Arabia. V. 52064.

FIG. 6. *Cymopolia* (*Karreria*) sp. Thin-section fragment to show sporangia, etc., ×50. Palaeocene-Lower Eocene, Sinjar Formation ; Pila Spi, Sulemania Liwa, Iraq. V. 52065.

FIGS. 7, 8. *Dissocladella deserta* sp. nov. Syntypes. 7. Longitudinal section, ×50. V. 52066. 8. Transverse section, ×50. V. 52067. Palaeocene-Lower Eocene, Umm er Rudhama Formation ; Aidah and Wagsa, Diwaniyah Liwa, Iraq.

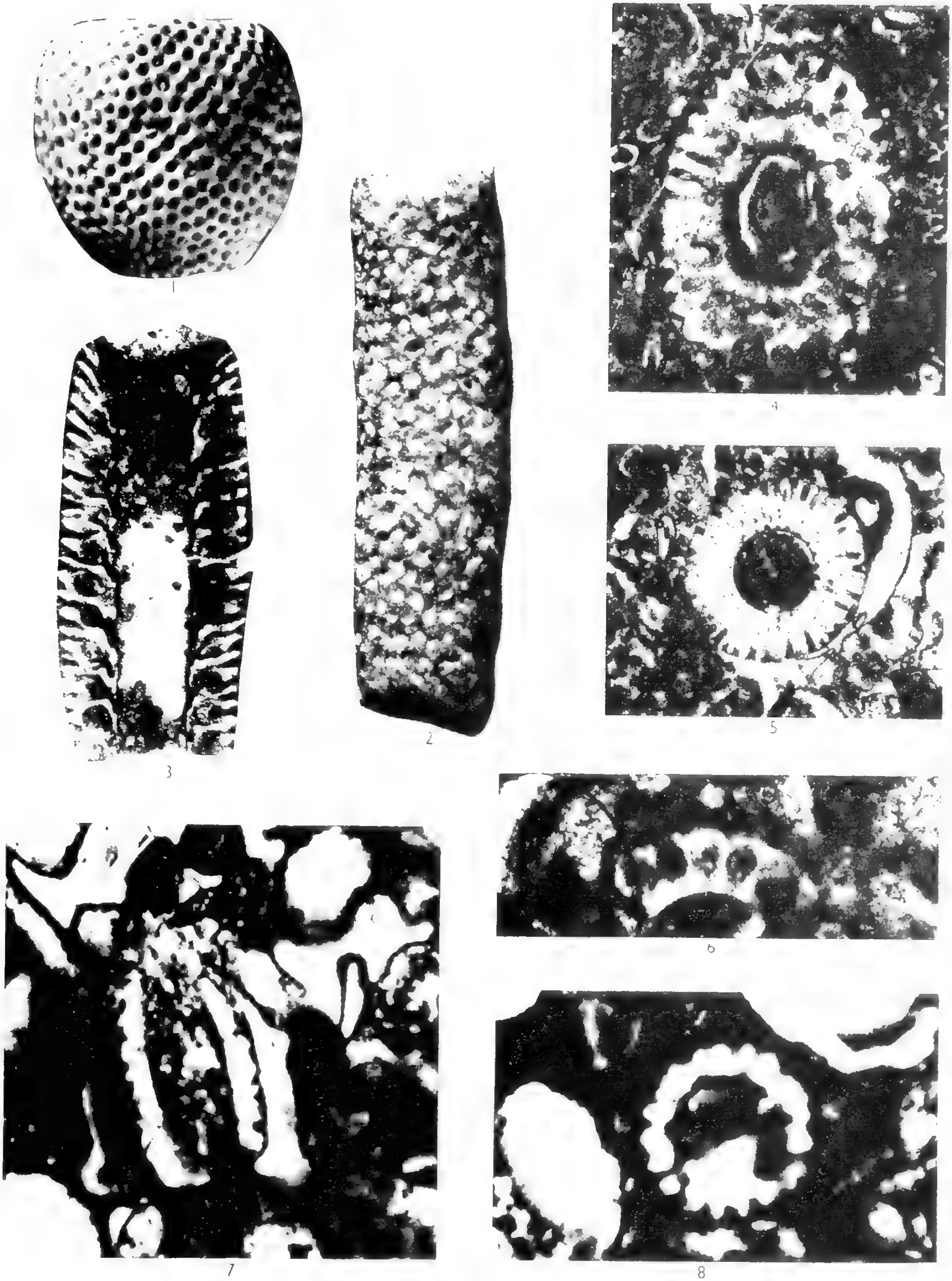

1
2
3
4
5
6
7
8

PLATE 11

Dissocladella, Furcoporella

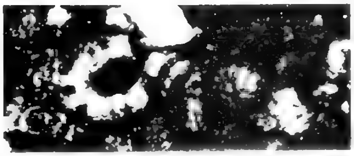
FIGS. 1–3. *Dissocladella savitriae* Pia. 1. Transverse section, ×28. Palaeocene, Sinjar Formation ; Banik, Mosul Liwa, Iraq. V. 41580. 2. Fragment to show enlarged wall-structure, thin-section, ×50. Palaeocene, Kolosh Formation ; Rowanduz, Erbil Liwa, Iraq. V. 52068. 3. Broken solid specimen to show nodose-annular external appearance, ×28. Lower Eocene ; subsurface, Dukhan No. 3 Well ; Qatar, Arabia. V. 52069.

FIGS. 4–6. *Dissocladella undulata* (Raineri) Pia. Thin-sections. 4. Transverse section, ×50. V. 52070. 5, 6. Near-longitudinal sections, ×50. V. 52071. Cretaceous, Turonian, Sadi Formation, subsurface, Musaiyib No. 1 Well, Hill Liwa, Iraq.

FIGS. 7–9. *Furcoporella diplopora* Pia. 7. Oblique-longitudinal section to show successively divergent pore-pairs (lower part of figure), ×38. V. 41606. 8. Longitudinal section to show waisted pores, ×30. V. 41606. 9. Transverse section to show paired branches, ×45. V. 51232. Palaeocene-Lower Eocene, Kolosh Formation ; Sedelan, Sulemania Liwa, Iraq.

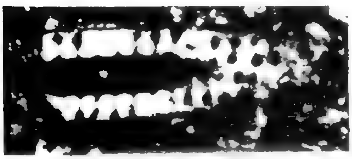
1

3

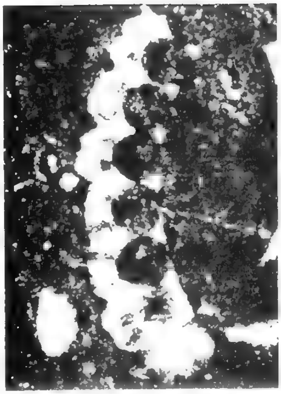


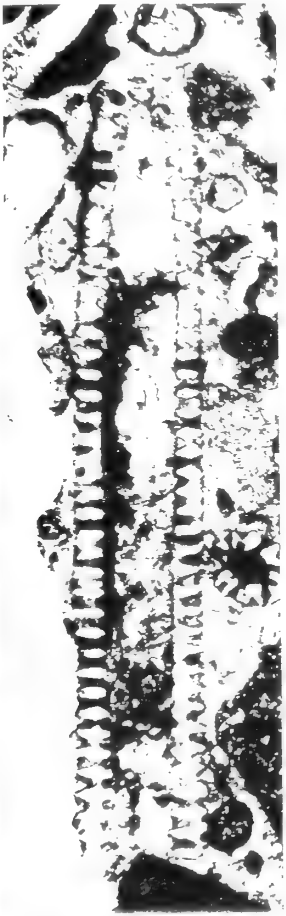
4

5



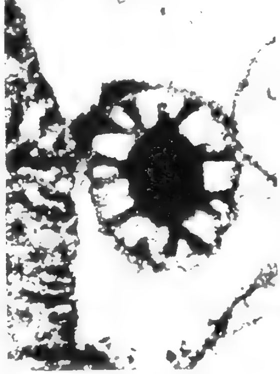
6





8

7



9

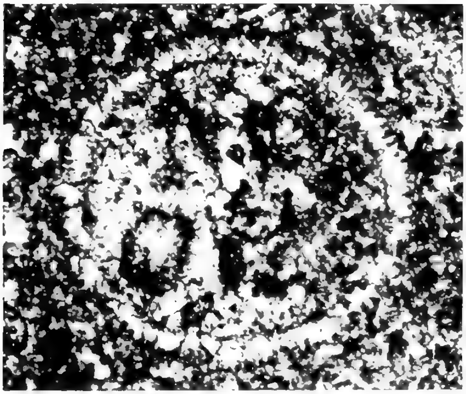
PLATE 12

Griphoporella, Indopolia

FIGS. 1, 3. "*Griphoporella arabica* Pfender" (*Ovulites maillolensis* Massieux). Transverse and oblique longitudinal sections, ×50. Palaeocene-Lower Eocene; Sahil Maleh, Batinah Coast, Oman, Arabia. V. 52033.

FIG. 2. *Indopolia satyavanti* Pia. Oblique-longitudinal section showing sterile whorls, ×50. Palaeocene-Lower Eocene, Sinjar Formation; Banik, Mosul Liwa, Iraq. V. 52072.

FIG. 4. *Griphoporella* cf. *perforatissima* Carozzi. Tangential section of wall-fragment, ×50. Upper Jurassic, Najmah Formation; subsurface, Kirkuk Well No. 117, Iraq. V. 52073.



1

2

3

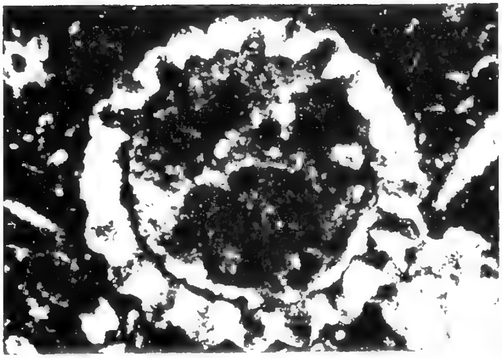
4

PLATE 13

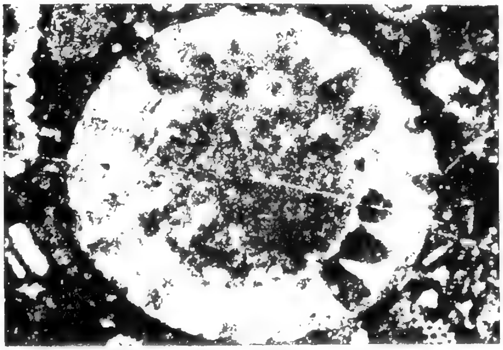
Mizzia

Figs. 1–5. *Mizzia velebitana* Schubert, thin-sections of separate bead-like units or segments, ×28. 1. Slightly oblique longitudinal section. V. 52074. 2, 3. Typical transverse sections near equatorial region. V. 52075, V. 41575. 4. Random sections, the lower suggests externally roofed branch-pores. 5. Three random sections : the upper is of a pear-shaped segment cut longitudinally. V. 52076. Permian, Darari Formation ; fig. 3 from Harur, the others from Ora, both localities in Mosul Liwa, Iraq.

1



2



3

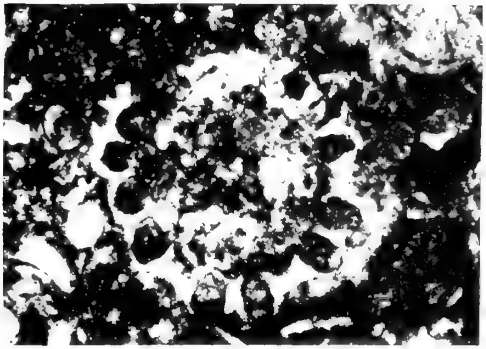
4

5

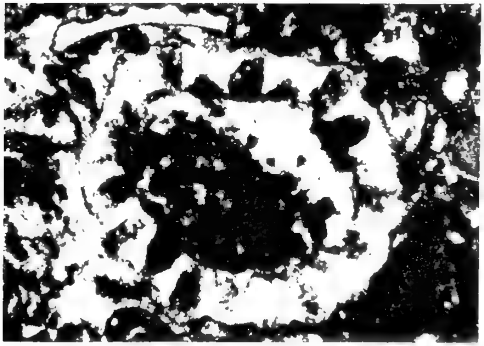
PLATE 14

Mizzia

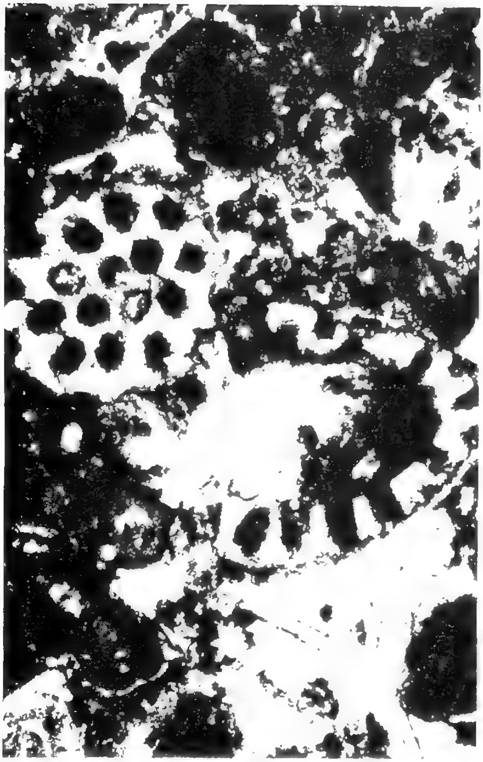
FIGS. 1–4. *Mizzia velebitana* Schubert, thin-sections. 1. Transverse cut of unit with roofed pores, ×28. 2. Longitudinal-oblique section of unit, ×28. 3. Tangential cut to show typical coarse "colander-pore" pattern; also longitudinal section of broken unit, ×28. 4. Random section of *Mizzia*-rock, ×20. Permian, Darari Formation; Ora, Mosul Liwa, Iraq. V. 52076.



1



2



3

4

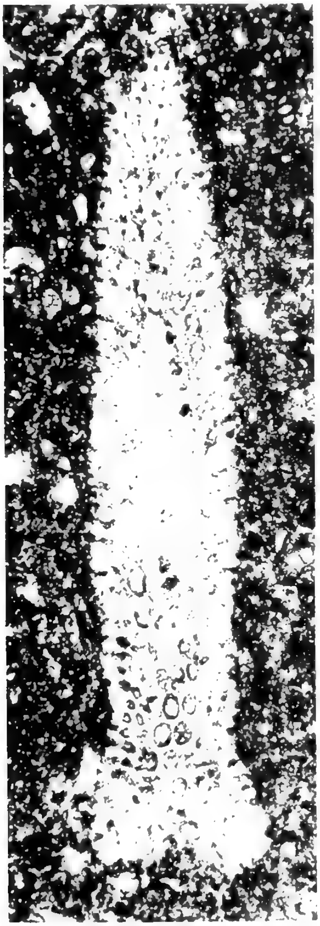
PLATE 15

Neomeris, Munieria

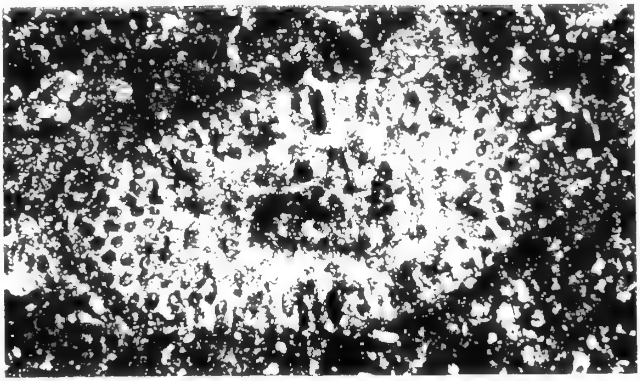
FIG. 1. *Neomeris cretacea* Steinmann. Oblique-longitudinal section, ×20. Cretaceous, Maestrichtian, Bekhme Formation ; Chia Gara, Mosul Liwa, Iraq. V. 52077.

FIG. 2. *N. cretacea*. Oblique-transverse section, ×28. Cretaceous, Campanian-Maestrichtian, Aqra-Bekhme limestone facies ; Gal-i-Mazurka, Mosul Liwa, Iraq. V. 41585.

FIGS. 3–8. *Munieria baconica* Deecke. Typical fragmentary remains, thin-sections, ×50. 3, 4, 6. Cretaceous, Aptian level, Qamchuqa Formation ; Ru Kuchuk, Mosul Liwa, Iraq. V. 52078. 5, 7. Cretaceous, Barremian level, Sarmord Formation ; Sarmord, Sulemiania Liwa, Iraq. V. 52079. 8. Cretaceous, Aptian-Albian level, Qamchuqa Formation ; Surdash, Sulemania Liwa, Iraq. V. 52080.

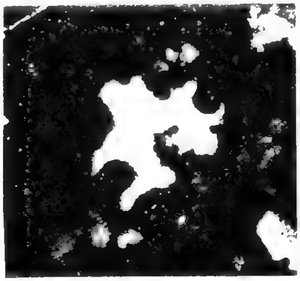


1



2

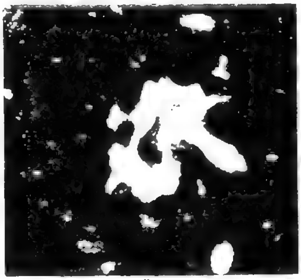
3



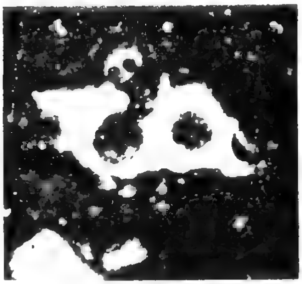
4

5

6



7



8

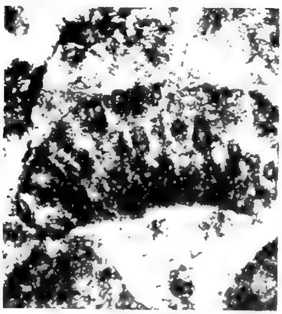
PLATE 16

Palaeodasycladus

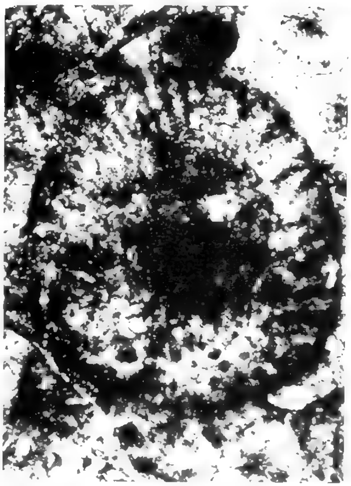
FIGS. 1–5. *Palaeodasycladus mediterraneus* Pia. 1, 2. Longitudinal, and two transverse sections, ×20. V. 52081. 3. Fragment to show detail of branch-constrictions, ×28. V. 52082. 4. Oblique-transverse cut to show effect of angle of branch-inclination. V. 52082. 5. Detail of terminal branches, ×20. V. 52083. Jurassic, Lias, Lower Musandam Formation ; Wady Bih, Qamar, Peninsular Oman, Arabia.

1

2



3



4

5

PLATE 17

Permoperplexella, Pianella, Pagodaporella

FIGS. 1–5. *Permoperplexella attenuata* gen. et sp. nov., thin-sections, ×28. 1. Paratype, oblique-longitudinal cut. V. 52084. 2, 3. Paratypes, oblique section of distal end, oblique-transverse cut near this end. V. 52085. 4. Holotype, longitudinal section. V. 52085. 5. Oblique-transverse cut near distal end. V. 52085. Permian, Zinnar Formation ; Ora, Mosul Liwa, Iraq.

FIGS. 6–8. *Pianella pygmaea* (Gümbel) Radoičić. 6. Transverse section, ×40. V. 52086. 7. Longitudinal section, ×40. V. 52087. 8. Oblique section, ×40. V. 52088. Cretaceous, Valanginian, Garagu Formation ; subsurface, Mileh Tharthar Well No. 1, Dulaim Liwa, Iraq.

FIGS. 9, 10. *Pagodaporella wetzeli* Elliott. 9. Longitudinal thin-section of solid, dissociated, example, ×60. V. 41605. 10. Solid example, external appearance, ×60. V. 41604. Palaeocene, Kolosh Formation ; Bekhme, Erbil Liwa, Iraq.

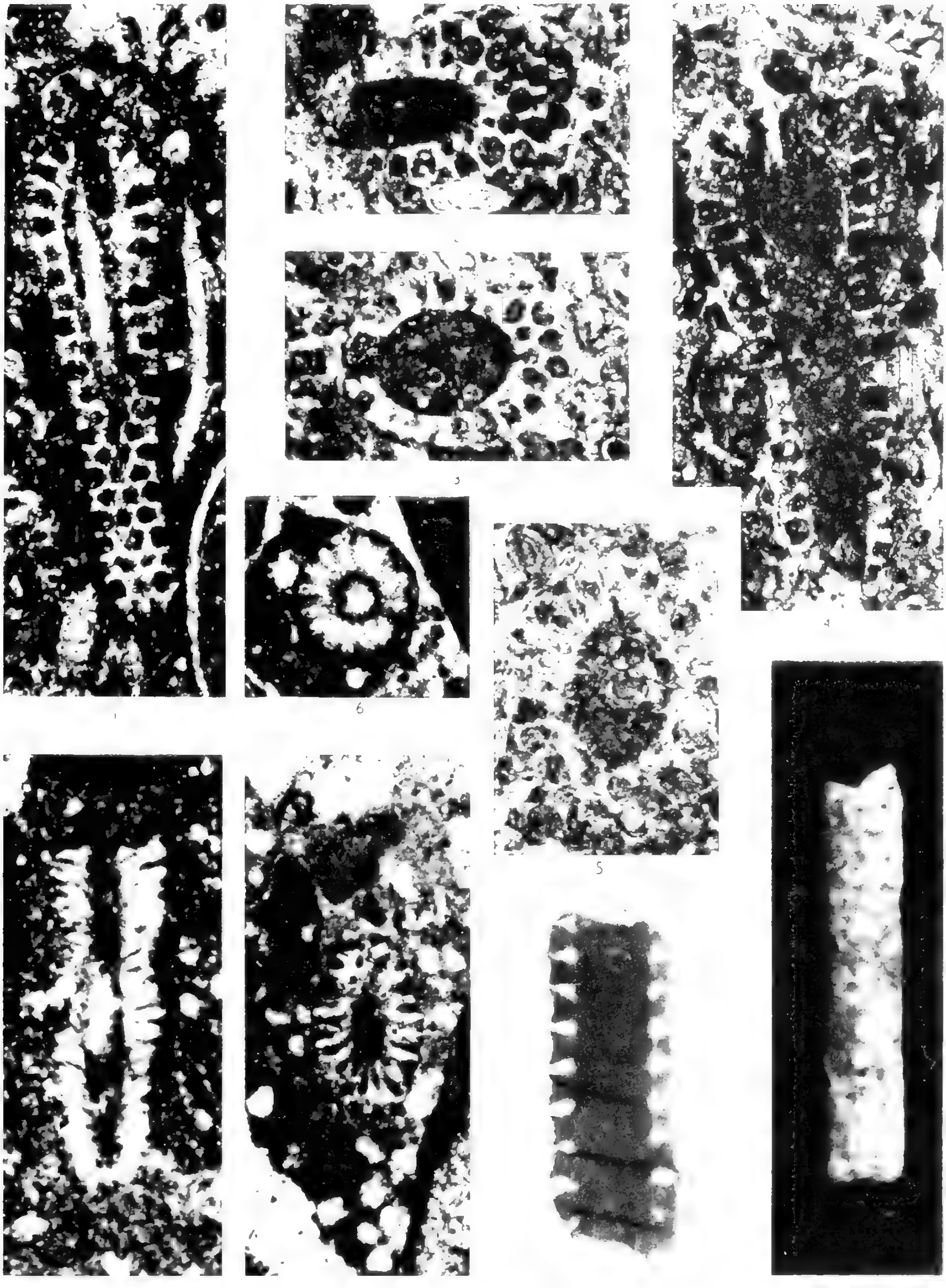


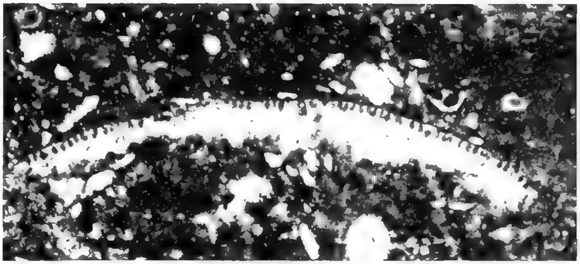
PLATE 18

Pseudoepimastopora

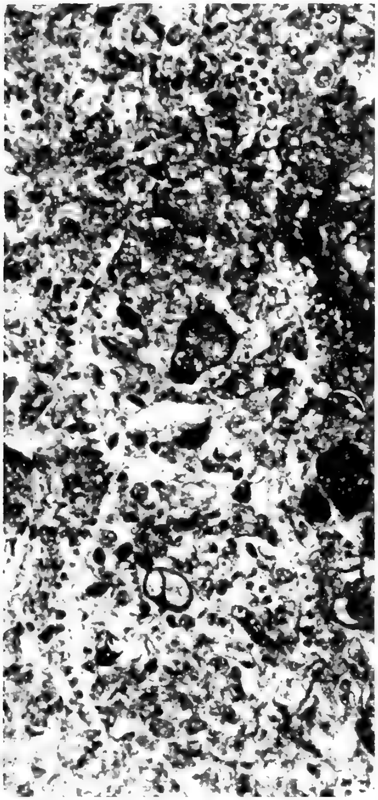
FIGS. 1, 2. *Pseudoepimastopora ampullacea* sp. nov. 1. Holotype, longitudinal section of "waxing-and-waning" example, ×30. V. 52089. 2. Paratype, random section of long curved piece of thallus, ×30. V. 52090. Permian, Zinnar Formation; Ora, Mosul Liwa, Iraq.

FIGS. 3, 4. *Pseudoepimastopora* cf. *likana* Kochansky and Herak. Fragments of wall-material showing large distinctive pores, thin-sections, ×30. Permian; Jebel Qamar, Peninsular Oman, Arabia. V. 52091, 52092.

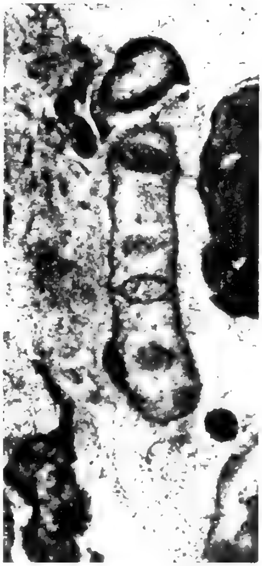
FIGS. 5–7. *P. ampullacea*. 5, 6. Thin-sections of wall-fragments showing clearly the form of the pores, ×60. V. 52093. 7. Transverse section, ×60. V. 52094. Permian, Zinnar Formation; Ora, Mosul Liwa, Iraq.



2

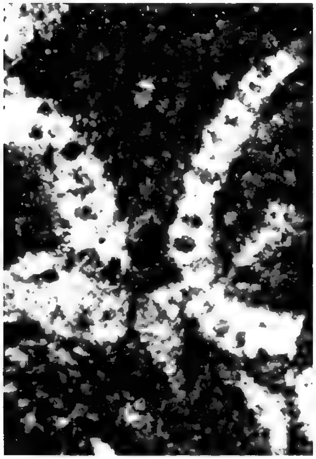


1

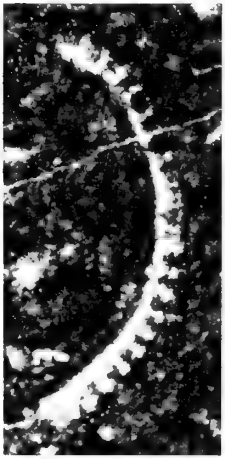


3

4



5



6

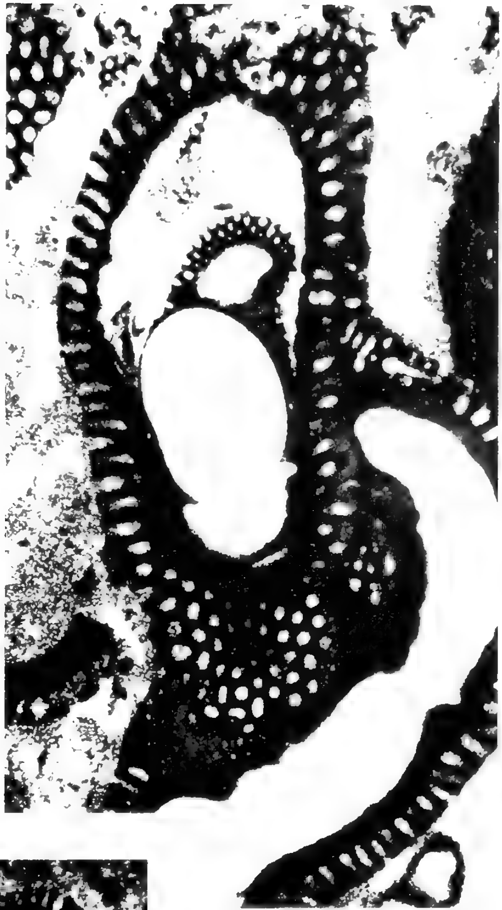
7

PLATE 19

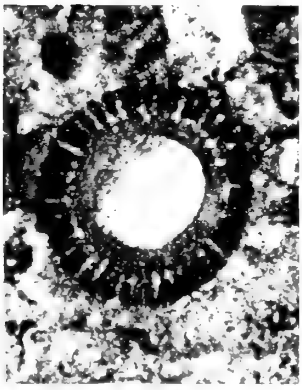
Pseudovermiporella

FIGS. 1–5. *Pseudovermiporella sodalica* Elliott. Thin-sections, ×50. 1, 2. Portions of large individuals showing typical coarse mesh of main tube, supposed diagenetic lining layers, inner tube and irregular meandriform growth ; in fig. 2 mesh of a second small individual is seen in position of growth on the inner tube of the main individual. V. 41641, V. 41645, 3. Transverse cut of typical single unattached tube. V. 41644. 4, 5. Sections of small early clusters or " nucleo-conch " structures ; in fig. 4 the reniform, calcite-filled structure is unusually large but is apparently an early inner tube. 41649, 41642. Permian; Jebel Qamar, Peninsular Oman, Arabia.

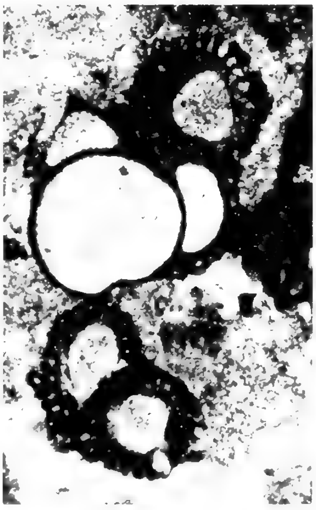
1



2



3



4

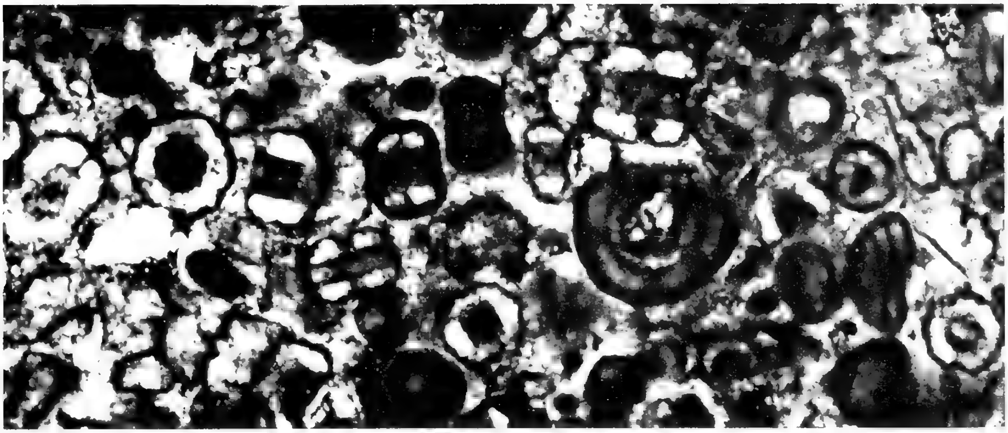
5

PLATE 20

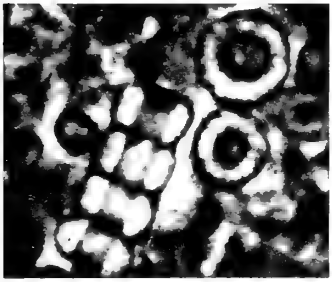
Salpingoporella

FIGS. 1, 2, 5. *Salpingoporella apenninica* Sartoni & Crescenti. Thin-sections, ×50. 1. Random vertical and transverse cuts of short lengths of tube. V. 52095. 2, 5. Longitudinal sections with associated transverse sections. V. 52096. Upper Jurassic, Najmah Formation ; subsurface, Kirkuk Well No. 117, Iraq.

FIGS. 3, 4, 6, 7. *Salpingoporella annulata* Carozzi. 3. Oblique-vertical section, ×50. V. 52097. 4. Transverse section, ×50. V. 52099. 6. Solid (dissociated) specimen, external appearance, ×50. V. 52099. 7. Longitudinal thin-section, ×50. V. 52098. Upper Jurassic, " Arab Zone " ; subsurface, Dukhan Well No. 28 (figs. 3, 4, 7) and Well No. 2 (fig. 6), Qatar, Arabia.

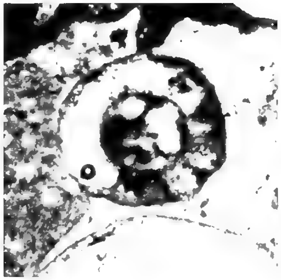


1



2

3



4

5

6

7

PLATE 21

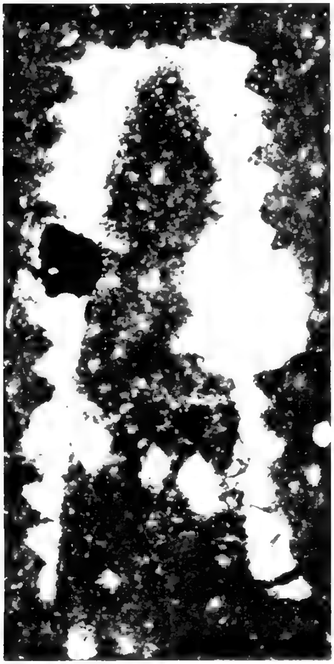
Salpingoporella

FIG. 1. *Salpingoporella arabica* sp. nov. Paratype, oblique-longitudinal thin-section, wall replaced by clear calcite, ×50. Cretaceous, Albian-Cenomanian level, top Qamchuqa Formation ; Sarmord, Sulemania Liwa, Iraq. V. 52100.

FIG. 2. *S. arabica.* Paratypes, oblique-transverse sections to show simple branch-structure, ×50. Lower Cretaceous, Upper Musandam Formation ; Jebel Hagab, Peninsular Oman, Arabia. V. 52101.

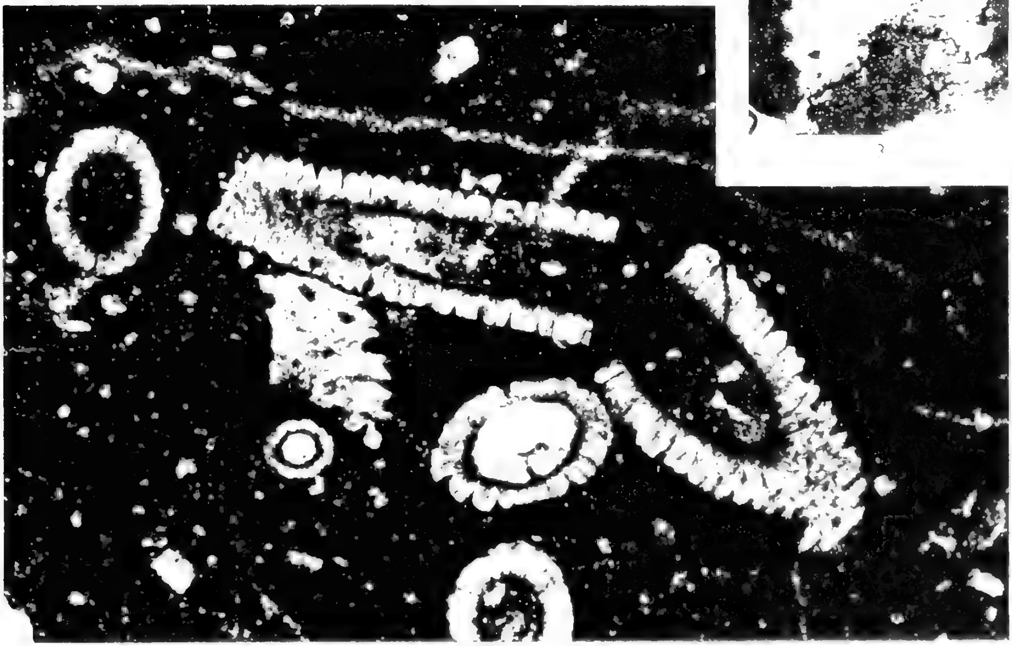
FIG. 3. *S. arabica.* Holotype, longitudinal section, ×40. Cretaceous, Aptian-Albian level, Qamchuqa Formation ; Surdash, Sulemania Liwa, Iraq. V. 52102.

FIG. 4. *Salpingoporella dinarica* Radoičić (*Hensonella cylindrica* Elliott). Numerous typical random cuts in thin-section, ×50. Cretaceous, Barremian-Aptian level, Sarmord Formation ; Sekhaniyan, Surdash, Sulemania Liwa, Iraq. (Compare preservation with that of *S. arabica* above). V. 52103.



2

3



4

PLATE 22

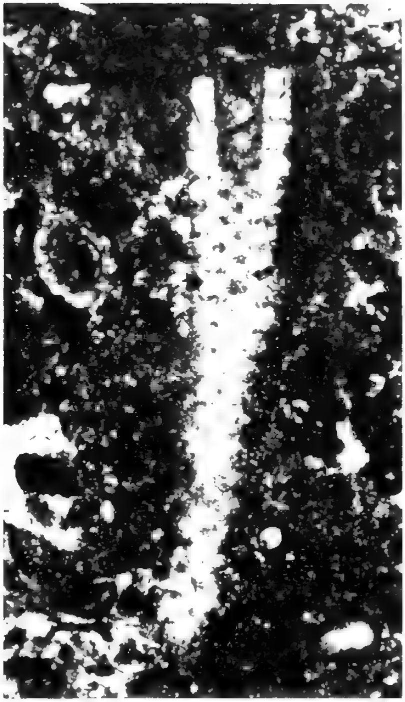
Salpingoporella dinarica (Hensonella)

FIG. 1. Part of the type thin-section, ×30, of *Hensonella cylindrica* Elliott. Cretaceous, Barremian, Qamchuqa Formation ; Sarmord, Sulemania Liwa, Iraq. Z. 902.

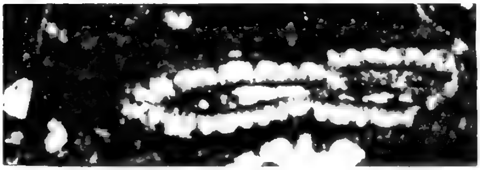
FIG. 2. *S. dinarica* Radoičić. Thin-section ×50, oblique-longitudinal cut, to show dasyclad branch-pore pattern as described by Radoičić. Cretaceous, Upper Aptian ; Djebel Amsid, Constantinois, Algeria. V. 52104.

FIGS. 3–6. Thin-section cuts, ×50. 3. Crushed example to show continuity of inner thin dark layer. V. 52103. 4. Random sections, one crushed. V. 52103. 5. Longitudinal and transverse sections showing very regular fibrous radial structure and coarser features with external widening interpreted as dasyclad branches. V. 52103. 6. Transverse section showing the inner dark layer of organism incrusted by a thin irregular coating of transparent calcite, the interior being filled with darker marly-calcareous matrix. V. 52105. Cretaceous, Barremian-Aptian level, Sarmord Formation ; Sekhaniyan, Surdash, Sulemania Liwa, Iraq.

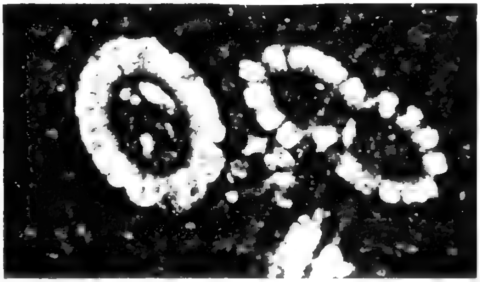
1



2



3



4

5

6

PLATE 23

Terquemella, Thyrsoporella

FIGS. 1, 2. *Thyrsoporella silvestrii* Pfender. 1. Transverse section, ×50. V. 52106. 2. Longitudinal section, ×50. V. 52107. Middle Eocene; Jebel Tanamir, Fatah, Oman, Arabia.

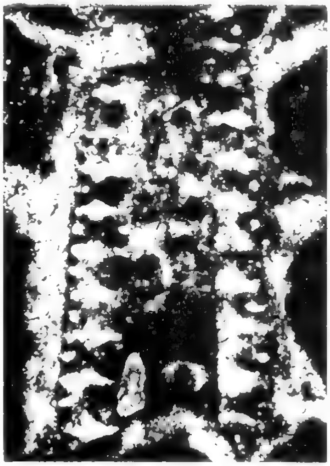
FIG. 3. *T. silvestrii*. Tangential-longitudinal section, ×50. Palaeocene-Lower Eocene, Kolosh Formation; Sedelan, Sulemania Liwa, Iraq. V. 52108.

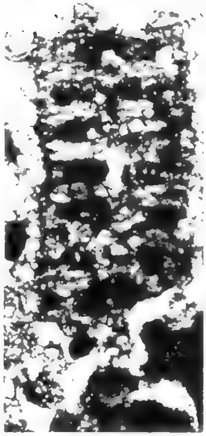
FIG. 4. *T. silvestrii*. Longitudinal section of large individual, ×28. Middle Eocene; Jebel Tanamir, Fatah, Oman, Arabia. V. 52109.

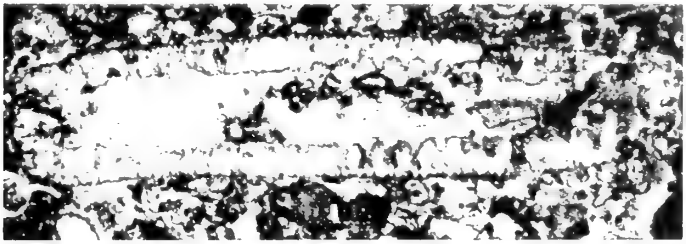
FIG. 5. *Terquemella globularis* Elliott. Solid specimen to show exterior, ×80. Palaeocene, Kolosh Formation; Bekhme, Erbil Liwa, Iraq. V. 41603.

FIGS. 6, 7. *Terquemella bellovacensis* Munier-Chalmas. 6. Tangential-transverse section, ×55. V. 41589. 7. Vertical section, ×55. V. 41590. Palaeocene-Lower Eocene, Sinjar Formation; Sirwan, Sulemania Liwa, Iraq.

FIG. 8. *T. globularis*. Thin-sections, ×55. Palaeocene-Lower Eocene, Sinjar Formation; Sirwan, Sulemania Liwa, Iraq. V. 32496.



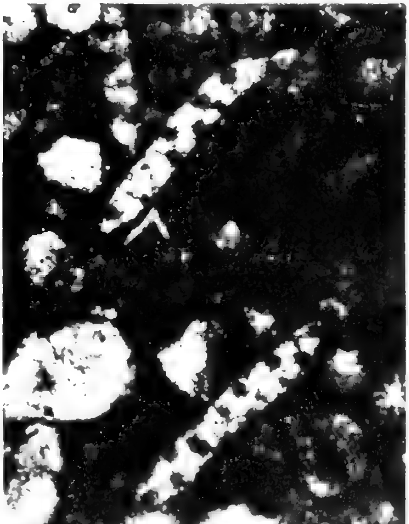




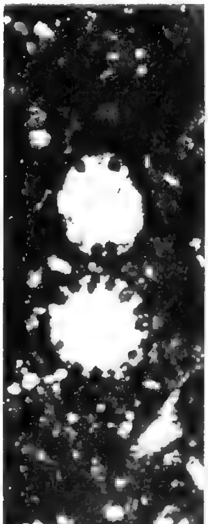
4

5

6



7



8

PLATE 24

Thyrsoporella, Trinocladus

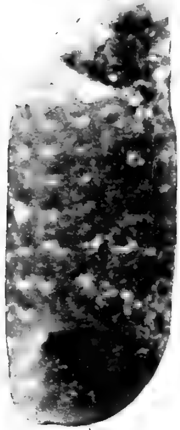
FIGS. 1, 2, 6, 7. *Trinocladus perplexus* Elliott. 1. Solid specimen to show exterior, ×50. V. 52117. 2. Longitudinal section of specimen in which an example of the codiacid *Ovulites morelleti* Elliott perfectly fits the stem-cell cavity of the larger fossil, ×50. V. 52110. 6. Oblique and transverse sections, ×50. V. 52114. 7. Near-longitudinal section to show branch-structure, ×50. V. 52115. Palaeocene-Lower Eocene, Kolosh Formation ; Koi Sanjak, Erbil Liwa, Iraq.

FIG. 3. *Trinocladus tripolitanus* Raineri. Longitudinal section, ×50. Cretaceous, Turonian ; subsurface, Ras Sadr Well No. 1, Trucial Oman, Arabia. V. 52111.

FIG. 4. *T. tripolitanus*. Oblique-transverse section, ×50. Cretaceous, Turonian, Sadr Formation ; Musaiyib Well No. 1, Hilla Liwa, Iraq. V. 52112.

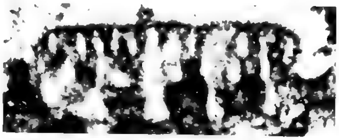
FIG. 5. *Thyrsoporella silvestrii* Pfender. Thin-section fragment to show detail of branch-structure, ×50. Middle Eocene ; Jebel Tanamir, Fatah, Oman, Arabia. V. 52113.

FIG. 8. *Trinocladus radoicicae* sp. nov. Syntypes, transverse sections, ×50. Cretaceous, Maestrichtian, Tanjero Formation ; Diza, Erbil Liwa, Iraq. V. 52116.


1

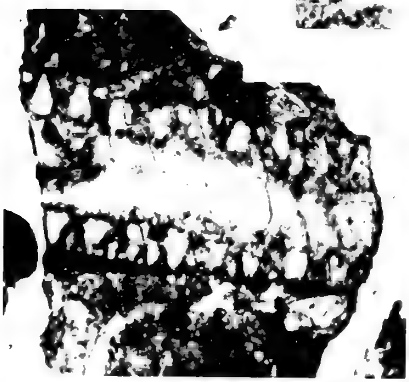

3

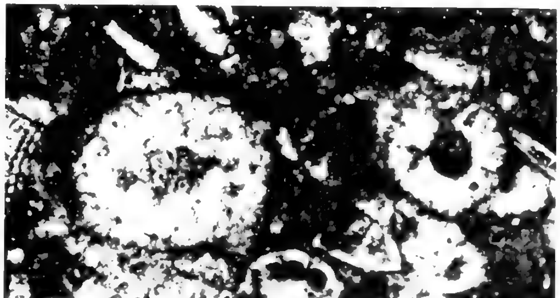

4


5


2


6


7


8

Printed in England by Staples Printers Limited at their Kettering, Northants, establishment